Molecular Phylogenetics and Evolution 112 (2017) 107–121

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

The niche and phylogeography of a passerine reveal the history of biological diversification between the Andean and the Atlantic forests

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ARTICLE INFO

Article history:
Received 21 October 2016
Revised 25 March 2017
Accepted 28 March 2017
Available online 3 April 2017

Keywords:
Andean forest
Atlantic forest
Chaco
Cerrado
Approximate Bayesian Computation
Gallery forests

ABSTRACT

The Atlantic Forest is separated from the Andean tropical forest by dry and open vegetation biomes (Chaco and Cerrado). Despite this isolation, both rainforests share closely related lineages, which suggest a past connection. This connection could have been important for forest taxa evolution. In this study, we used the Saffron-billed Sparrow (*Arremon flavirostris*) as a model to evaluate whether the Andean and the Atlantic forests act as a refugia system, as well as to test for a history of biogeographic connection between them. In addition, we evaluated the molecular systematic of intraspecific lineages of the studied species. We modeled the current and past distribution of *A. flavirostris*, performed phylogeographic analyses based on mitochondrial and nuclear genes, and used Approximate Bayesian Computation (ABC) analyses to test for biogeographic scenarios. The major phylogeographic disjunction within *A. flavirostris* was found between the Andean and the Atlantic forests, with a divergence that occurred during the Mid-Pleistocene. Our paleodistribution models indicated a connection between these forest domains in different periods and through both the Chaco and Cerrado. Additionally, the phylogeographic and ABC analyses supported that the Cerrado was the main route of connection between these rainforests, but without giving decisive evidence against a Chaco connection. Our study with *A. flavirostris* suggest that the biodiversity of the Andean and of the Atlantic forests could have been impacted (and perhaps enriched?) by cycles of connections through the Cerrado and Chaco. This recurrent cycle of connection between the Andean and the Atlantic Forest could have been important for the evolution of Neotropical forest taxa. In addition, we discussed taxonomic implications of the results and proposed to split the studied taxon into two full species.

1. Introduction

According to the refugia hypothesis (Haffer, 1969; Haffer and Prance, 2001), Pleistocene climate cycles have driven speciation by promoting contraction, fragmentation and expansion of rainforest ranges, which in turn allowed for vicariance, divergence and secondary contact. Most discussions concerning the refugia hypothesis have been focused on the intra biome level, for example within the Amazon or within the Atlantic Forest (Cabanne et al., 2016; Carnaval et al., 2009; Maldonado-Coelho et al., 2013; Thomé et al., 2010), and less attention has been given to processes occurring among related but fully isolated forest biomes, such as the Andean and Atlantic forests or the Caatinga and Chaco dry forests (Batalha-Filho et al., 2013; Costa, 2003; Pennington et al., 2004; Werneck, 2011).

The Andean and the Atlantic forests (Fig. 1) are among the most diverse forest biomes in the world (Orme et al., 2005). They are currently isolated from each other by dry forests and open-vegetation domains: the Chaco and the Cerrado, respectively. In

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http://dx.doi.org/10.1016/j.ympev.2017.03.025
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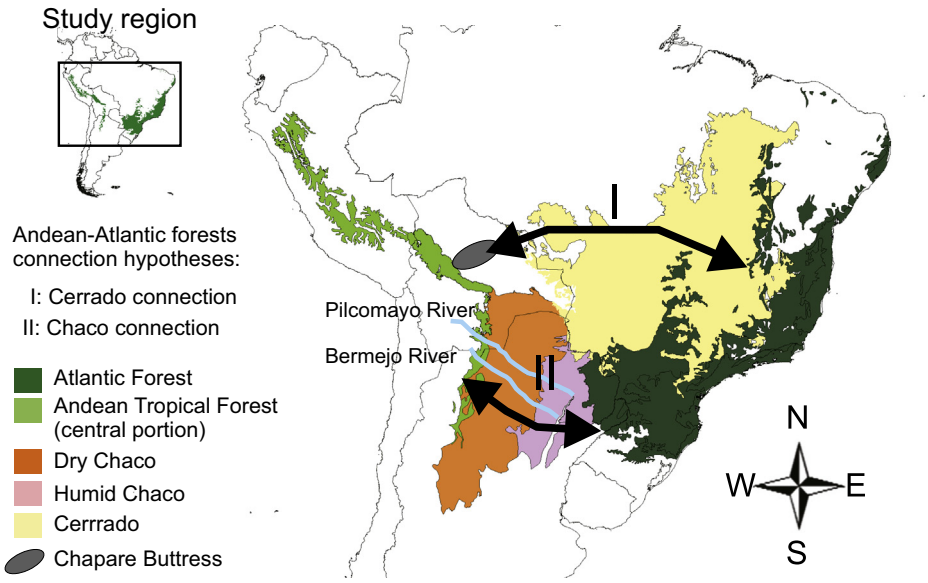

Fig. 1. Geographic distribution of the central Andean Tropical Forest, the Atlantic Forest, Cerrado and Chaco. The working hypotheses on the historical pathways between the Atlantic and the Andean forests are indicated.

spite of this isolation, they share closely related lineages of rainforest dependent organisms (Faivovich et al., 2004; García-Moreno et al., 1999; Nores, 1992; Olrog, 1963), many of them do not have a continuous range but belong to the same species in both biomes, which indicated that these rainforests have been connected in the past (Chapman, 1926). This connection is also suggested by palynological studies (Ledru, 1993, 1991; Oliveira-Filho and Ratter, 1995), which indicate that wet forest expanded into the Cerrado and towards the Andes during the last glacial maximum, a phenomenon that could have connected forest domains. However, neither the frequency nor the type of connection between regions –i.e., if through continuous or stepping stone forests– have been studied until now.

Thus, the Andean and the Atlantic forests could act as a refugia system, and therefore their past range dynamics could have been important in the process of avian diversification in the Neotropics. Because these forested biomes are currently isolated, they might be at the isolation phase of the cycle of a refugia system. If their connection dynamics (i.e., cycles of connection and isolation) prompt cycles of vicariance and divergence, the species present in both domains should show a deep phylogeographic gap between domains, because major diversification events should have occurred between regions. Alternatively, if the dynamic of the connection allow for high and constant rates of historical gene flow, enough to preclude divergence, the shared organisms should not present a significant population gap between regions.

More specific biogeographic aspects of the connection between the Andean and Atlantic forests are still unknown, such as the geological processes involved, timing and regions that bridged these rainforests. One of the main hypothesis to explain the connection between these forests state that the contact could have occurred in the Chaco region, through gallery forests along main rivers (i.e., Bermejo and Pilcomayo Rivers, Fig. 1) that expanded during interglacial periods (from now on Chaco connection) (Nores, 1992; Olrog, 1963; Smith, 1962). The Chaco connection hypothesis is mostly based on forest bird distribution patterns, and up to now there is not enough evidence from other scientific areas supporting extensive expansions of wet forests in the Chaco (Zurita et al., 2014). Alternatively, Silva (1994) proposed that instead of through the Chaco and its main rivers, the connection occurred during glacial maxima through the southern Amazon forest and through expansions of forests into the Cerrado (from now on Cerrado connection). Forest expansions in the Cerrado are supported by some palinological studies (Ledru, 1993, 1991; Oliveira-Filho and Ratter, 1995), as well as by niche models of the Atlantic Forest biome (Carnaval and Moritz, 2008; Sobral-Souza et al., 2015) and of its organisms (Cabanne et al., 2016; Thomé et al., 2010).

We are not aware of any study specifically oriented to test alternative hypotheses on the Andean-Atlantic forests connection. These hypotheses could be tested by niche models and phylogeographic studies of rainforest species that are present in both regions. For instance, species distribution models would help to test connection routes by estimating potential distributions of forest taxa across different geographic regions and periods (Elith and Leathwick, 2009; Soberon and Peterson, 2005). Also, from the genetic standpoint and a cladistic biogeography paradigm, the phylogenetic position of populations occurring in-between the Andean and the Atlantic forests would shed light onto the biogeographic history of both regions. For instance, if samples of wet forest taxa from gallery forests in the Chaco (e.g., along the Pilcomayo and Bermejo rivers, Fig. 1) are sister groups to populations from the Andes or from the Atlantic Forest, a connection through the Chaco would be supported.

In this paper we studied the Saffron-billed Sparrow (*Arremon flavirostris*) to evaluate the contact between these forest domains. *A. flavirostris* inhabits the understory of moist and semideciduous forests of the base of the central Andes and of the interior Atlantic Forest, as well as gallery forests of the eastern Chaco and of the central and southern Cerrado (Fig. 2a) (Rising, 2011). Although strict categorization of Andean-Atlantic forests core species versus Andean-Atlantic-gallery forests species is simplistic, we view *A. flavirostris* as not strictly Andean-Atlantic forests core species. However, it is a good study model to evaluate the working hypotheses on the Andean-Atlantic forests connection because it inhabits both the moist forest domains and the gallery forests (i.e., at the Bermejo and Pilcomayo Rivers, Figs. 1 and 2) that could have been directly involved in bridging the moist domains. The characterization of the evolutionary relationships of populations from these gallery forests is essential to understand the biogeographic processes that occurred between forest domains. In addition, the species is interesting from the taxonomic standpoint, because (i) it has been suggested to form a superspecies with

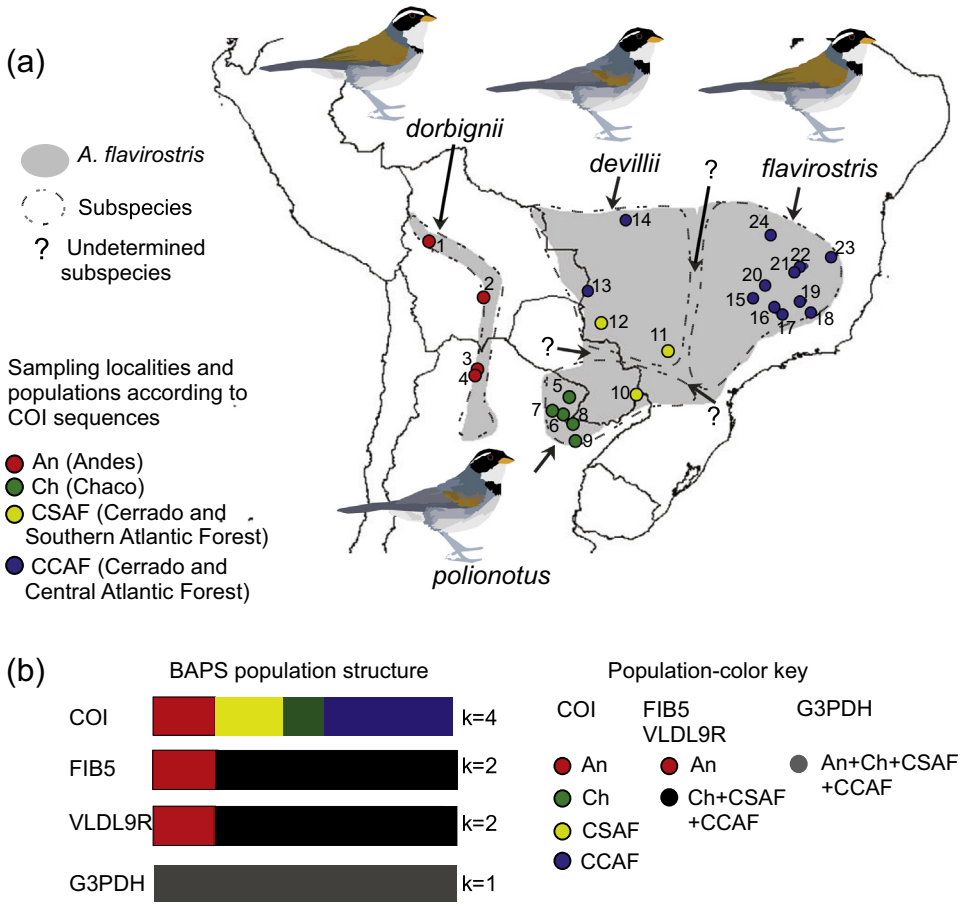

Fig. 2. (a) Sampling localities for the phylogeographic study of *Arremon flavirostris*. Subspecies distribution, plumage variation and populations identified with COI sequences in BAPS are also shown. See full identification of localities in Appendix A Table A.1. (b) Bayesian analysis of population genetic structure (BAPS) based on the COI, FIB5, VLDL9R and G3PDH sequences. Colors indicate different genetic clusters. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

A. taciturnus, *A. aurantiirostris*, *A. schlegeli* and *A. abeillei* (Rising, 2011); and (ii) because there are four subspecies described according to plumage variation (Fig. 2), but there is not any study addressing if these subspecies are independent evolutionary lineages (but see Buainain et al., 2016). Some of these subspecies lack a clear diagnosis and do not have a well defined geographic distribution (Fig. 2a; Buainain et al., 2016; Hellmayr, 1938; Silva, 1991).

The main goal of this study is to address whether the Andean and the Atlantic forests act as a refugia system, as well as to evaluate biogeographic hypotheses on the connection between them (i.e., Chaco and Cerrado connection, Fig. 1). To achieve our goals we modeled the current and past distribution of *A. flavirostris*, performed phylogeographic analyses and tested biogeographic scenarios by using Approximate Bayesian Computation (Beaumont et al., 2002), where specific questions were: (1) what does niche modeling indicate about the connection routes between rainforests; (2) is there a strong phylogeographic gap located between the Andean and the Atlantic forests?; (3) what is the phylogenetic position of samples from the humid Chaco (localities 5–9, Fig. 2a)?; and (4) are the subspecies of *A. flavirostris* independent evolutionary lineages?

2. Material and methods

2.1. Ecological niche models

To study the Andean-Atlantic forests connection we modeled distribution maps of *A. flavirostris* by using MAXENT (Phillips et al., 2006). MAXENT niche models are built from presence and background data, and perform well relative to other distribution modeling approaches (Elith et al., 2006). We compiled occurrence records from our own field work, from Museu de Zoologia de Minas Gerais (Universidade Federal de Minas Gerais, Brazil), Museo Argentino de Ciencias Naturales (Buenos Aires), and from the Global Biodiversity Information Facility (GBIF; www.gbif.org). To reduce spatial autocorrelation, we randomly removed occurrence records that were less than 10 km apart from each other, which resulted in a final data-set of 95 records. See MAXENT input file in Supplementary Material I.

For the MAXENT analyses we used the 19 climate variables available at WordClim 1.4 (Hijmans et al., 2005), with a resolution of 2.5 arc min and delimited by the following rectangle: north-eastern corner x = −30.5325 and y = −1.2614 and south-western corner x = −61.1071 and y = −36.1285. Seven bioclimatic variables (BIO1, BIO4, BIO6, BIO7, BIO16, BIO17 and BIO18) were selected for the final analysis by first rejecting highly correlated variables (Peterson et al., 2011), and then by selecting relevant variables by a rationale of permutation importance >5%. General conditions for analyses were: random test points = 25; replicates = 10; replicate type: subsample; maximum iterations = 5000. We validated current models by evaluating AUC values (Pearson et al., 2007).

We projected the niche model to three past periods: (1) mid-Holocene (6000 years before present –ybp–), with two climate models: CCSM4 (Community Climate System Model) and MIROC-ESM (http://www.worldclim.org/paleo-climate); (2) Last Glacial Maximum (LGM, 21,000 ybp), past climate models: CCSM3 (Com-

munity Climate System Model, available at: http://www.ccsm.ucar.edu) and MIROC (Model of Interdisciplinary Research on Climate, available at: http://www.ccsr.utokyo.ac.jp/kyosei/hasumi/MIROC/tech-repo.pdf); and (3) Last Interglacial (LIG, 120,000 ybp) (Otto-Bliesner et al., 2006). We obtained binary maps by using a threshold of equal training sensitivity and specificity.

2.2. Samples for the genetic study

We sampled 56 *A. flavirostris*, covering 24 localities of the entire species distribution and subspecies spectrum (Fig. 2a). We took special attention in sampling localities in between the Andean and the Atlantic forests that are in the putative corridors between regions (Nores, 1992; Silva, 1994): localities 12–14 at western Cerrado; and localities 5–9, which are associated to the gallery forests of the Pilcomayo and Bermejo Rivers, in the Chaco. It is worth noting that localities 5–9 are key to our study because they are located where the Andean and the Atlantic forests are at their closest point. To confirm the monophyly of the focal species we constructed a phylogeny that sampled its putative most closely related species (Raposo, 1997; Sick, 1986): *A. aurantiirostris, A. semitorquatus, A. schlegeli* and *A. franciscanus*. See Appendix A Table A.1 for information on the samples and sequences used in this study.

2.3. DNA amplification and sequencing

DNA was purified from muscle, blood or toe pads. DNA from fresh tissue was extracted following a glass fiber-based extraction protocol (Ivanova et al., 2006). DNA from toe pads was purified in an isolated laboratory, using a DNeasy Blood & Tissue Kit (QIAGEN) and with the addition of Dithiothreitol to the digestion buffer in a final concentration of 11 mg/ml.

We studied two mitochondrial genes: Cytochrome *c* oxidase subunit I (COI, 678 bp) and Cytochrome *b* (CytB, 978 pb). Because we were unable to get clean CytB sequences in about 50% of the samples, these sequences were only used to estimate a substitution rate for COI (see below). We also studied three nuclear markers: intron 5 of the Autosomal Beta-Fibrinogen gene (FIB5, 534 bp), intron 9 of the Z-linked Low Density Lipoprotein Receptor gene (VLDL9R, 400 bp), and intron 11 of Glyceraldehyde-3-Phosphodehydrogenase (G3PDH, 258pb). See primers and PCR conditions in Supplementary Material II, and GenBank accession numbers in Appendix A Table A.1.

Nuclear sequences that contained heterozygous indels were analyzed to resolve haplotypes by using the algorithm Process Heterozygous Indels in CodonCode Aligner v. 3.7 (Codon Code Corp., Dedham, MA). Also, we resolved the gametic phase of nuclear markers without indels by using PHASE (Stephens and Donnelly, 2003), as implemented in DnaSP (Librado and Rozas, 2009). We used the PHI test (Bruen et al., 2006), as implemented in SplitsTree4 (Huson and Bryant, 2006), to test for genetic recombination.

2.4. Phylogenetic and divergence time estimations

We performed Bayesian Inference (BI) and Maximum Likelihood (ML) phylogenetic analyses. First, to confirm monophily of *A. flavirostris*, we analyzed a concatenated sequence of COI and VLDL9R (total 1078 bp). Second, to study relationships within *A. flavirostris* we analyzed a concatenated sequence of COI, FIB5, VLDL9R and G3PDH (total 1870 bp). We analyzed heterozygous sites in nuclear markers as polymorphic characters, and not as ambiguous sites (N). We used MrModelTest (Nylander, 2004) and the Akaike information criterion to select nucleotide substitution models: for COI, model HKY + I; for FIB5, GTR + I; for VLDL9R, HKY and for G3PDH, GTR.

BI analyses were performed in MRBAYES 3.1 (Ronquist and Huelsenbeck, 2003), with two parallel runs, using one 'cold' and three 'hot' chains, for a total of 50 million generations and sampling every 1000 generations. The alignments were partitioned by DNA marker, analyzed under the best-fit model for each partition, and allowing different rates across regions. We used a 25% burn-in and a 50% majority rule consensus tree was calculated to obtain the posterior probabilities for each node. We used GARLI 2.0 (Zwickl, 2006) for ML phylogenetic analyses, with a search of 50 million generations. The best fit model of molecular evolution was considered for each marker, and nodal support was evaluated with a nonparametric bootstrap (500 replicates).

We used BEAST 1.8 (Drummond et al., 2012) to estimate node divergence times. We used unlinked substitution rates and clocks across partitions, a Yule tree prior, constant population size, and a relaxed uncorrelated lognormal clock for each gene tree. For COI, we used a calibration rate obtained by comparison to CytB in BEAST equal to 1.34×10^{-2} substitutions/site/million years (s/s/Myr), assuming for CytB a substitution rate of 1.05×10^{-2} s/s/Myr (Weir and Schluter, 2008). For FIB5 and G3PDH, and for

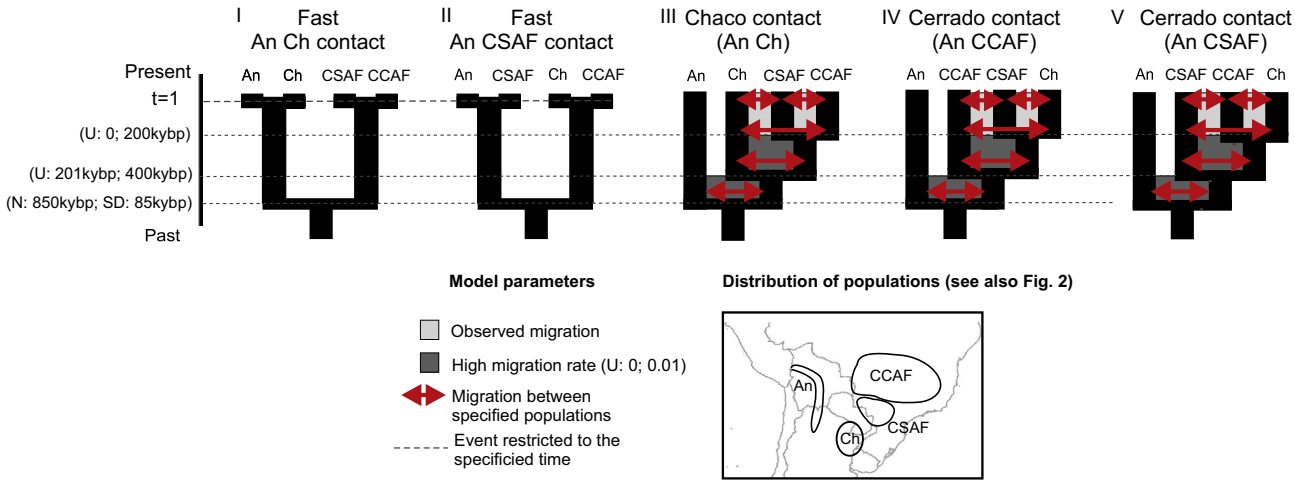

Fig. 3. Demographic models of *Arremon flavirostris* tested by Approximate Bayesian Computation analysis. Demographic models varied according to the population structure, gene flow and population split times. Time of demographic events (in thousands of years before present, kybp) are fixed or taken from a uniform (U) or normal (N) distribution with specific standard deviation (SD). Population acronyms are according to Fig. 2a.

VLDL9R, we used a substitution rate of 1.35×10^{-3} s/s/Myr and of 1.62×10^{-3} s/s/Myr, respectively (Ellegren, 2007). The final analysis used a burn-in of 10%, 100 million of generations, and sampled every 1000 generations.

We estimated divergence time and gene flow between populations using all the genetic markers with the IMa2 software (Hey and Nielsen, 2004; Nielsen and Wakeley, 2001). We did two sets of analyses. First, because the IMa2 infile requires a resolved topology, and the population phylogeny was not fully resolved, we performed three different runs, each with one of the possible resolved four-population topologies (Fig. 3, models III–V). Since the three runs produced comparable results, we chose randomly a run to provide the parameters of interest. Second, because we were unable to get full confidence interval for the divergence time between the Andes and the Atlantic populations, we also used a two-populations model to estimate this specific time parameter. The two-population model violated one assumption of the IMa2 analysis, because the mtDNA was not panmictic (Fig. 2). However, we considered time and gene flow values as valid because they overlapped with those point estimations obtained with the above mentioned four-population models. General conditions of the analysis were: -q50, -t6.5, -m4, -b2000000, -l0.5, -d1000, -kfg, -hn40, -ha0.99 and -hb0.75. We assumed a generation time of one year and converted coalescent times to years according to user's manual and the same substitution rates used in the BEAST divergence time analysis.

2.5. Population genetic structure

We employed BAPS v6.0 (Corander et al., 2008) to estimate the most likely number of genetically differentiated populations. For each marker we surveyed the probability of different number of genetic clusters (K = 1 to K = 20) under the models of "mixture analysis" and "spatial clustering of individuals". To further asses population genetic structure we estimated uncorrected distances, performed an Analysis of Molecular Variance (AMOVA) and estimated pairwise Φ_{st} values in ARLEQUIN 3.5 (Excoffier and Lischer, 2010).

2.6. Population genetic metrics

We estimated for each marker and population the nucleotide (π) and haplotype (h) diversity in DNAsp 5.1 (Librado and Rozas, 2009). We also estimated for each population the multilocus diversity parameter θ (theta), using the Extended Bayesian Skyline Plot approximation in BEAST. For estimating current θ-values we used all markers (except cytB) and similar analytical conditions used for the divergence time analysis in BEAST, with the exception of using a strict molecular clock (Heled and Drummond, 2010). Additionally, to test for deviation from neutral evolution or constant population size, we estimated Tajima's D (Tajima, 1989) in DNAsp 5.1 (Librado and Rozas, 2009).

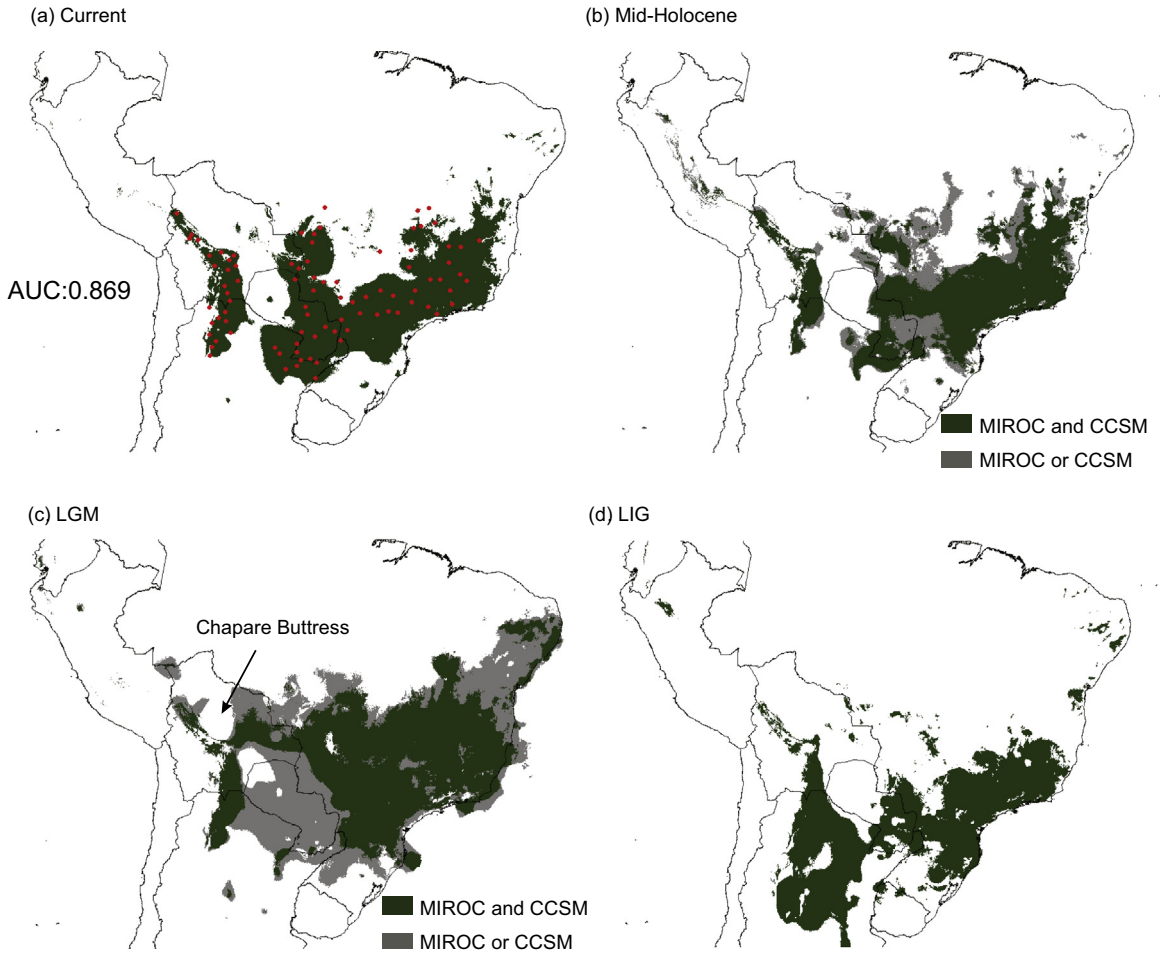

Fig. 4. Models of geographic distribution of *Arremon flavirostris* obtained in MAXENT. (a) Current. (b) Holocene (6000 ybp); (c) Last Glacial Maximum (LGM, 21,000 ybp); and (d) Last Inter-Glacial period (LIG, 130,000 ybp). Species records used in MAXENT are indicated in red. In (b) and (c) green areas represent overlapping between climate models (MIROC and CCSM), and grey areas represent a single climate model (MIROC or CCSM). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.7. Testing biogeographic scenarios using ABC

We used an Approximate Bayesian Computation (ABC) approach (Beaumont et al., 2002) to explore the fit of the observed genetic data to hypothetical population models of the contact between the Andean and the Atlantic forests. For this test, we considered clusters described by BAPS and with COI sequences as demographic units (populations, Fig. 2). The evaluated models considered putative different population scenarios product of contacts between the Andes and Atlantic Forest populations (Fig. 3). It is worth mentioning that each scenario tested could have been originated by vicariance or dispersion between regions. We interpreted sharing a common most recent ancestor between populations as evidence of connection between regions. Specifically, populations CCAF and CSAF (Figs. 1 and 2) included samples from gallery forests at the Cerrado, thus they represent a link through the Cerrado. Also, population Ch had samples from gallery forests associated to the main rivers of Chaco (Figs. 1 and 2), thus it represents a link through the Chaco. We also used null models (Models I and II of Fig. 3), where we expected a non-significant fit of the observed data. In addition, we explored models where populations were arranged in an island system, without any hierarchical relation-

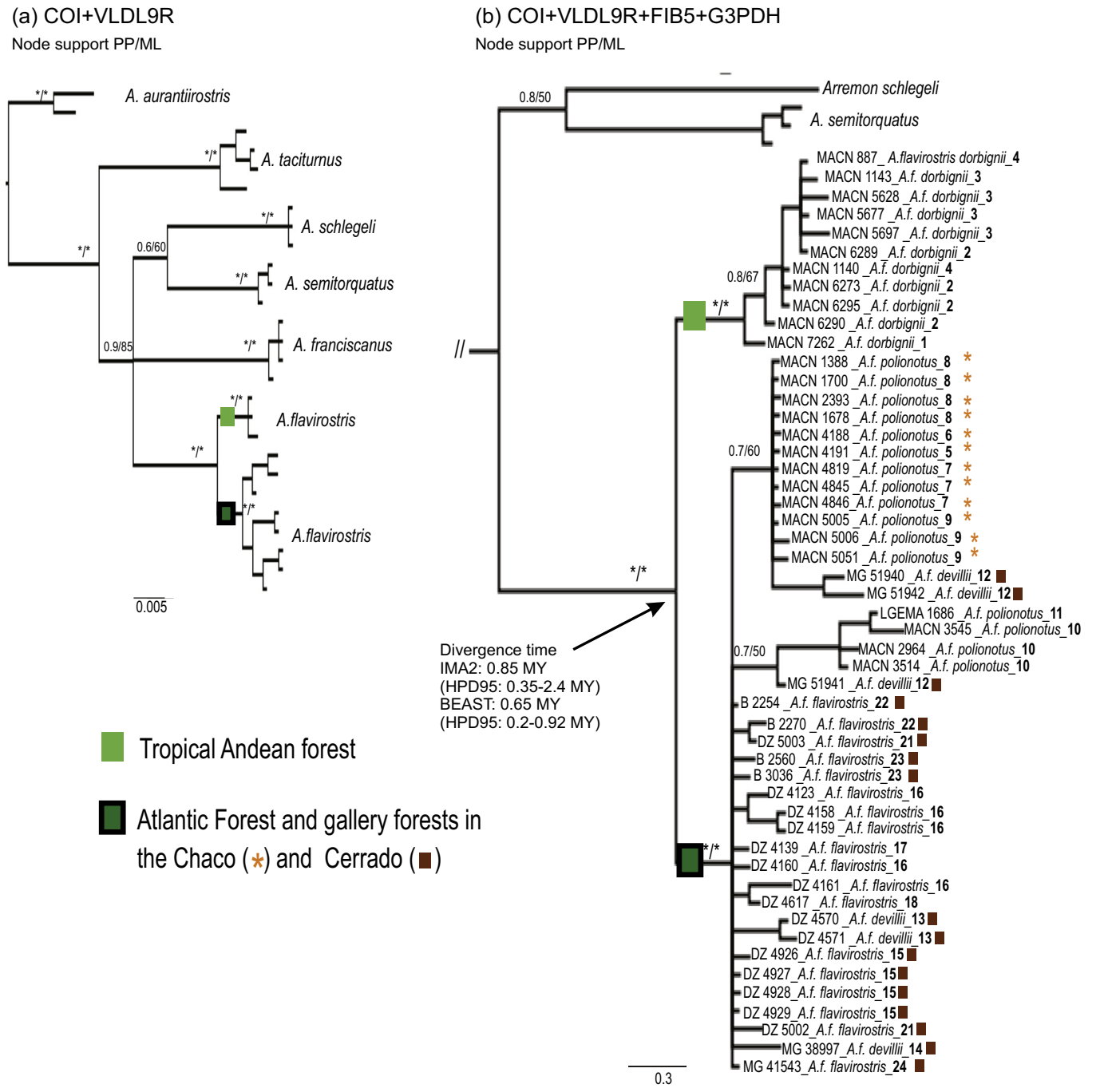

Fig. 5. (a) BI phylogenetic tree of *Arremon flavirostris* and allies obtained with COI and VLDL9R sequences (total 1078 pb). (b) BI intraspecific phylogenetic tree of *Arremon flavirostris* obtained with markers COI, FIB5, VLDL9R and G3PDH (total 1870 bp). Node support is indicated as posterior probability (PP) and maximum likelihood bootstrap scores (ML, 500 replicates). */* indicates maximum node support. Divergence time is in millions of years (MY). Sample labels represent tissue number, subspecies and sampling locality number of Fig. 2a (in bold). See Appendix A Table A.1 for further details on samples and localities.

ships among populations. However, we did not consider the results of these island models because the test was inconclusive. See Supplementary Material II for full results. Finally, we did not thoroughly explore double contact scenarios (e.g., through Cerrado and Chaco) because the assay was not conclusive too.

For coalescent simulations we only modeled the most variable markers (COI, FIB5 and VLDL9R). For each model and marker, we performed 100,000 coalescent simulations using BayeSSC (Anderson et al., 2005). Current migration, divergence time between the Andean and the other populations, the effective size of each population and marker were estimated in IMa2 and then used as input for the simulations. See in Supplementary Material II an example of infile for BayeSSC, as well as values used for effective sample size and observed migration.

The ABC test used 45 summary statistics obtained from the three markers data-set. For each marker we used 15 summary statistics from populations of Fig. 2: pairwise F_{st} between the Andes and each of the other three populations, and for individual populations Tajima's D, as well as h and π. We estimated posterior probabilities with the algorithm *mnlogistic* (Beaumont, 2010), and calculated model misclassification rates with *cv4postpr,* in the package *abc* for R and using a degree of tolerance of 0.01 (Csilléry et al., 2012). For model comparisons we evaluated Bayes factors (posterior probability ratios) according to Kass and Raftery (1995).

3. Results

3.1. Ecological niche models

The ecological niche model of *A. flavirostris* performed better than a random model (AUC = 0.869, Fig. 4a). The modeled distribution for the mid-Holocene was relatively similar to the current distribution, while models for the Late Pleistocene indicated significant changes in the distributions (Fig. 4c and d). During the LGM, *A. flavirostris* expanded toward the Cerrado, with some retraction in its southern distribution. In contrast, during the LIG, the species expanded into the current Chaco and contracted its range in the Cerrado. In general, these results support a double contact between the Andean and the Atlantic forests, through the Chaco and the Cerrado during different periods.

3.2. Monophyly of Arremon flavirostris

BI and ML analyses recovered *A. flavirostris* as monophyletic, with maximum support (Fig. 5a). Even though previous studies reported similar results (Barker et al., 2015; Klicka et al., 2014), only our study sampled the full intraspecific variation of the species, as well as all the closely related outgroups. For example, *A. franciscanus,* a species from southern Caatinga dry forests (Northeastern Brazil), was included in a phylogenetic study for the first time here. In the phylogeny of Fig. 5a, A. *flavirostris* is part of a polytomy involving *A. schlegeli, A. semitorquatus* and *A. franciscanus*, a relationship also indicated by other data-sets (Barker et al., 2015; Klicka et al., 2014), and that is in disagreement with the idea of *A. flavirostris* being sister to *A. taciturnus*, as suggested by Sick (Sick, 1986).

3.3. Intraspecific phylogeny and divergence time

BI and ML analyses recovered two main phylogroups in *A. flavirostris* (Fig. 5b): an Andean clade formed by samples from Bolivia and northwestern Argentina (subspecies *dorbignii*); and an eastern or Atlantic clade, formed by samples from the Atlantic Forest and gallery forests within the Cerrado and the humid Chaco (*devillii, polionotus* and *flavirostris*). The samples from the Chaco (localities 5–9 in Fig. 2) grouped together and were one of the most genetically distant from the Andean samples, which is not in agreement with the idea of a close relationship between those regions. The samples from gallery forest in the Cerrado are intermingled in the phylogram.

As nuclear markers did not present evidence of recombination ($P > 0.05$), we did not split them for the IMa2 and further analyses. The divergence between the Andean and Atlantic forests occurred during the Mid-Pleistocene: estimation with IMa2 = 0.85 (HPD95 = 0.348–2.4) millions of years (My); and with BEAST = 0.650 (HPD95 = 0.204–0.921) My. Gene flow estimations with IMa2 are very low, and indicated that the Andean subspecies (*dorbignii*) is completely isolated; migration (M) from Andes to Atlantic Forest = 0.0001 (HPD95 = 0–0.0115) individuals per generation, and M from Atlantic Forest to Andes = 0.0056 (HPD95 = 0–1.34) individuals per generation.

3.4. Population genetic structure and summary statistics

BAPS analyses with COI sequences identified four populations, while with the other markers one to two populations (Fig. 2a and b). Even though the number of populations varied among markers, COI, FIB5 and VLDL9R indicated the same phylogeographic gap between the Andean and the Atlantic forests. The difference in number of populations can be attributed to variable phylogeographic resolutions among markers as a product of different effective sizes and substitution rates. Therefore, we used the four-population structure described with COI for the downstream analyses (Fig. 2): (1) Andean (An), subspecies *dorbignii*; (2) Cerrado and Central Atlantic Forest (CCAF), with samples from the central region of the forested biome and gallery forests at central and eastern Cerrado (subspecies *flavirostris* and *devillii*); (3) Cerrado and Southern Atlantic Forest (CSAF), with samples from southern Atlantic Forest and gallery forests at southern Cerrado, as well as subspecies *devillii* and *polionotus*; and (4) Chaco (Ch), with samples from gallery forests of the humid Chaco of subspecies *polionotus*.

Table 1
Analysis of Molecular Variance (AMOVA) of *Arremon flavirostris*. Samples were grouped according to populations identified with COI sequences and the BAPS analysis. See details in Fig. 2.

Marker	Proportion of the variation (%)[PS]			Fixation indices		
	Among regions	Among populations, within regions	Within populations	F_{ct}	F_{st}	F_{sc}
COI	44.85	39.74	15.41	0.448**	0.845**	0.720**
FIB5	41.19	28.8	30.1	0.411**	0.614**	0.343**
VLDL9R	69.9	11.94	18.1	0.699**	0.770**	0.238**
G3PDH	−7.97	11.43	96.54	−0.079	0.034**	0.106*

[PS] Tested population structure: [(An), (CCAF, CSAF, Ch)].
* $P < 0.05$.
** $P < 0.01$.

The population genetic structure based on COI sequences was corroborated by the AMOVA and pairwise Φ_{st} analyses (Tables 1 and 2), which indicated for most markers that the highest proportion of the total genetic variation was allocated between the Andean and the Atlantic forests. Regarding the pairwise Φ_{st} values (Table 2, 50% of the markers indicated that the highest divergence occurred between the Ch and An populations, which did not support a close genetic link between those regions.

Table 3 presents summary statistics of *A. flavirostris'* populations. Populations An and CCAF are the most genetically diverse, according to the θ-values. There was a gradient of genetic diversity in the eastern part of the study region, with the highest diversity in the north (CCAF).

3.5. Testing biogeographic hypotheses with ABC

The ABC analyses tested five different scenarios (Fig. 3). The observed summary statistics used in these tests are presented in Tables 2 and 3. The specific ABC approach for model selection was conclusive because presented a low misclassification rate of 16 %, and because the negative controls received very low support (summed *P* for models I and II = 0.0317, Table 4). The two best-fit models invoked a Cerrado contact (models IV and V), whose summed *P* represented substantial evidence against a Chaco connection (summed *P* = 0.7475, Bayes factor = 3.39). These ABC results indicate that most of the data supported a Cerrado connection model, but without giving decisive evidence against a Chaco connection. Thus, the main connection between the Andean and Atlantic forests occurred through the Cerrado, and at the same time a minor connection could have occurred through the Chaco.

We also explored the working hypotheses with scenarios where populations were arranged in an island system. This analysis also recovered as the best-fit a model of Cerrado connection (Results shown in Supplementary Material II). However, we did consider these results because the test presented a high misclassification rate (34%).

4. Discussion

We studied the phylogeographic structure and paleodistribution of *A. flavirostris* to evaluate if the Andean and the Atlantic forests act as a refugia system, as well as to test connection scenarios between these rainforests. Our findings suggest that the Andean and the Atlantic forests act as a refugia system. Also, the results support that a main connection between these forests could have occurred through the Cerrado region, and that another connection could have occurred through Chaco.

Table 4
Approximate Bayesian Computation analysis for selecting demographic models of *Arremon flavirostris*. See model details in Fig. 3.

Model	Posterior probability *P**
I. Fast Ch contact (negative control)	0.0073
II. Fast CCAF contact (negative control)	0.0244
III. Chaco contact (An-Ch)	0.2208
IV. Cerrado contact (An-CCAF)	0.3638
V. Cerrado contact (An-CSAF)	**0.3837**

* *P*, posterior probability obtained in abc for R based on the algorithm *mnlogistic*. Best fit model is indicated in bold.

4.1. Biogeography of the Andean-Atlantic forests connection

The results with *A. flavirostris*, taken together, supported an Andean-Atlantic forests main connection through the Cerrado, as well as gave low support for a contact through the Chaco. Our findings are in accordance with previous studies on the contact between these two tropical forests (Chapman, 1926; Nores, 1992; Silva, 1991), with the exception that we propose the novel idea that biogeographic links through the Cerrado and Chaco are not mutually exclusive.

The phylogeographic study of *A. flavirostris* supported predictions of a Cerrado connection. First, even though the intraspecific phylogeny did not clearly evidence any contact route (Fig. 5b), the samples from the Chaco, which are geographically closest to the Andes, are one of the most genetically distant from the Andean samples (Table 3), which is not in agreement with the idea of a Chaco connection. Second, the ABC analysis supported as best-fit the models with Cerrado as corridor (Table 4 and Fig. 3). Finally, the northernmost Cerrado and Atlantic population (CCAF) presented the highest genetic diversity in the region, while the southernmost population (Ch) was the least diverse (Table 2). A higher genetic diversity in the CCAF population could imply a larger pop-

Table 2
Pairwise Φ_{st} between populations of *Arremon flavirostris* of Fig. 2a. The highest significant Φ_{st} value for each marker is indicated in bold.

Marker	Φ_{st} pairwise comparisons					
	An-CCAF	An-CSAF	An-Ch	CCAF-CSAF	CCAF-Ch	CSAF-Ch
COI	0.856*	0.8*	**0.914***	0.713*	0.65*	0.86*
FIB5	0.62*	**0.71***	0.65*	0.1	0.395*	0.43*
VLDL9R	0.73*	0.816*	**0.85***	0.19*	0.3*	0.2
G3PDH	0.044*	0.22	0.021	0.08	**0.05***	0.2

* P < 0.05.

Table 3
Genetic diversity and summary statistics of *Arremon flavirostris*' populations. Populations are based on BAPS analysis and COI sequences (Fig. 2a). Sample size (n), nucleotide (π) and haplotype (h) diversity, Tajima's D and the population genetic diversity parameter θ (theta) are indicated.

	Populations															
	Andean (An)				Cerrado and Central Atlantic Forest (CCAF)				Cerrado and Southern Atlantic Forest (CSAF)				Chaco (Ch)			
	COI	FIB5	VLDL9R	G3PDH	COI	FIB5	VLDL9R	G3PDH	COI	FIB5	VLDL9R	G3PDH	COI	FIB5	VLDL9R	G3PDH
n	11	22	18	20	22	34	38	38	7	12	12	12	12	20	18	24
π	0.002	0.002	0.0012	0.001	0.003	0.006	0.003	0.006	0.002	0.005	0.002	0.002	0.0004	0.004	0.001	0.001
h	0.763	0.558	0.242	0.195	0.889	0.721	0.753	0.635	0.809	0.560	0.703	0.752	0.303	0.368	0.526	0.201
D	−0.975	−0.270	−1.125	−1.512	−1.060	−0.643	−0.402	−1.703	−0.318	0.004	1.079	−5.905	−0.194	0.229	1.547	−1.256
Θ (95% CI)	1.15 (0.003–3.05)				0.91 (0.006–2.70)				0.78 (0.0002–1.90)				0.14 (0.0038–0.80)			

ulation effective size than in the Chaco, and therefore a higher probability of being source of migrants.

The phenotypic variation of *A. flavirstris* is in agreement with a Cerrado connection between the Andean and Atlantic forests. First, its plumage pattern is not compatible with a Chaco connection. Specifically, an olive-green back coloration can be considered a shared basal state (plesiomorphic) in *A. flavirostris* and allies (Fig. 5a), because it is a state present in the nearest outgroup (*A. taciturnus*) (Silva, 1991). Only the Andean (An) and the Cerrado CCAF population present an olive-green back, which in the latter population is polymorphic; i.e. birds from eastern CCAF have olive-green back and from the western range have grey back (Fig. 2a). CSAF and Ch populations have fixed grey backs. Therefore, the back coloration state shared between the An and the CCAF populations could be interpreted as a recent, or stronger, genetic link between regions, or as retention of ancestral character (Silva, 1991). But, the fact that the Ch population presented a derived character for the back (grey), different from the primitive state of the An population (olive), did not support a recent link between Chaco and the Andes. Second, a recent study on song variation of *A. flavirostris* indicate that only birds from northern Bolivia (La Paz) share song characters between the Andean and the Atlantic lineages (Buainain et al., 2016). All the other Andean populations, from central Bolivia to northwestern Argentina, have a distinct song in comparison to the Atlantic lineage. Because bird songs have an inherited component, even in an oscine bird with learned song like *A. flavirostris*, we interpreted this result as a support for a population link through northern Bolivia, and thus through the Cerrado.

A Cerrado connection is supported by other studies, such as palaeopalynological analyses in the Cerrado (Ledru, 1993, 1991; Ledru et al., 2015; Oliveira-Filho and Ratter, 1995), genetic studies of birds and mammals (Batalha-Filho et al., 2013; Costa, 2003) and by niche models of animals and plants (Bueno et al., 2016; Sobral-Souza et al., 2015; Werneck, 2011). Even though those studies do not directly show a connection between regions, they suggest that rainforests expanded into the Cerrado in recurrent occasions, making a connection through the region highly likely and supporting a scenario of multiple contacts as proposed here.

A Cerrado connection for Andean and Atlantic forests taxa could have existed through the Bolivian foreland for the last 10 million years. In order to understand the biogeographical connection between domains it is also necessary to take in account the geological history of the region, and not only forest dynamics. For at least the last 10 million years the shortest path between the Andes and the Brazilian shields has been the Bolivian Andean foreland basin, around the Chapare Buttress, northern of both the Pantanal basin and of the limit between the Amazon and the Paraná-Paraguay basins (Lundberg et al., 1998) (Fig. 1). Even though the Andean foreland basin is an unstable region in terms of river and megafan dynamics (Lundberg et al., 1998; Wilkinsona et al., 2006), its whole geological set up has been relatively stable since the mid Pliocene, after retraction of the Paranan Sea (Lundberg et al., 1998). This geological stage, coupled with forest dynamism associated to global glacial cycles, could have set up a scenario of biogeographic contact between regions. A connection through this specific region is supported by the niche models of *A. flavirostris*, which suggest that at the LGM the region presented suitable habitats for the species (Fig. 4c), and also by the genetic analysis that supported a contact through Cerrado. Interestingly, there are passerines showing a typical circum-Amazonian distribution (e.g. *Platyrhinchus mystaceus*) that present an almost continuous distribution at the region of the shortest distance between the Andes and the Brazilian shield (Remsen, 1991). Another contact point at the Bolivian Andean foreland could be along the hills with wet forest foci at the dry forest region of eastern Bolivia (Santa Cruz) known as Chiquitania. We propose this because there are a few records of *A. flavirostris* in the region, which actually represent one the closest records of the subspecies *devillii* to the Andes (Rising, 2011). Besides, according to the niche model of *A. flavirostris*, eastern Bolivia could have presented suitable conditions for the species during past periods like the LGM (Fig. 4c), making the Cerrado connection highly likely.

In addition to a Cerrado connection, a corridor through the Chaco is clearly suggested by the niche models when projected into the LIG (Fig. 4d). And, even though the genetic analysis gave substantial support for a Cerrado connection, it also suggests that a Chaco connection cannot be left unconsidered. Accordingly, a corridor through Chaco could have existed, but with less biographic importance than the alternative Cerrado corridor. For example, such a Chaco corridor could have lasted shorter or could have been narrower than a Cerrado corridor. An alternative explanation for the dissimilar support given by the niche models and the genetic analysis for a Chaco connection would imply that the Andean and Atlantic populations had been already reproductively isolation when contacted through a putative corridor in the Chaco. Under this scenario, the niche models would have indicated an effective population contact in the Chaco, but because gene flow could have been minimum or inexistent, the genetic analysis would have not supported such connection.

The evidence in favor of the existence of rainforest that could have allowed a Chaco connection during the Late Pleistocene is mixed. The few palaeobotanical and paleontological studies available for the Chaco indicate that its characteristic dry vegetation has been present for most of the Pleistocene (Contreras et al., 2015; Zurita et al., 2014, 2009), and that the course of their rivers and associated gallery forests have been very unstable (Adamoli et al., 1990; Ramella and Spichiger, 1989; Sennhauser, 1991; Wilkinsona et al., 2006), but also suggest the existence of short periods with humid and tropical climates (Turchetto-Zolet et al., 2016; Zurita et al., 2014), which might have allowed short periods of wet forest expansions and bouts of gene flow in rainforest organisms. More studies on the Pleistocene history of Chaco are needed to evaluate their paleoenvironments and to confirm the presence of stable humid forests (e.g., gallery or continue forest) that could have allowed establishment of wet forest species in the region.

4.2. Andean and Atlantic forests as a refugia system

Our study supports that the Andean and the Atlantic forests act as a refugia system, and therefore that their current isolation and past geographic dynamics are important for the evolution of forest-dwelling taxa. Accordingly, we expected to find a strong phylogeographic divergence in *A. flavirostris* between these forest domains, which was supported by the data. Also, we expected that the paleodistribution models indicated a continuous distribution between the Andean and the Atlantic forests, which is also supported (Fig. 4).

Other forest taxa with allopatric populations restricted to both the Andean and Atlantic forests present their deepest phylogeographic gap between these regions (Faivovich et al., 2005, 2004; Nores, 1992; Pavan et al., 2014; Percequillo et al., 2011; Ribas and Miyaki, 2007; Rocha et al., 2014), in agreement with our results. Even though the number of studied taxa is very low, there seems to be heterogeneity across taxa in the temporal divergence between populations restricted to each forest, which suggest that multiple biogeographic contacts could have occurred between these regions (Smith et al., 2014). For instance, the divergence between the Andean and the Atlantic populations in a sample of three of passerines varied from 1.5 My (*Elaenia obscura*), to about 1 My and 0.15 My (*Syndactylla rufosuperciliata* and *Pipraidea melanonota*, respectively) (Cabanne et al., unpublished; Chaves et al., 2008; Lavinia, 2016; Rheindt et al., 2008). Additional examples of taxa with a strong phylogeographic gaps between the Andean and the Atlantic

forests are hylid frogs (Faivovich et al., 2005, 2004), some sister taxa of cricetid rodents (Percequillo et al., 2011), woodcreepers of the genus *Lepidocolaptes* (Arbeláez-Cortés et al., 2012) and parrots of the genus *Pionus* (Ribas and Miyaki, 2007).

A scenario of multiple biogeographic contacts between the Andean and the Atlantic forests is also suggested by the paleodistribution models of *A. flavirostris*, as well as by the cyclical nature of glaciations. Our paleodistribution models (Fig. 4) suggested contact through Cerrado during the LGM, and likely through Chaco during LIG. These paleodistribution models only spanned the last 0.120 My, but because at least the last five glacial cycles have been similar in time interval and intensity (Lisiecki and Raymo, 2005), the modeled scenarios of Fig. 4 could have been recurrent across the Quaternary. Therefore, the Andean and the Atlantic forests could have been connected during multiple occasions in the past, and species shared between these forests could have undergone recurrent cycles of vicariance, divergence and secondary contacts. These cycles could have been significant to drive evolution of these organisms and or to allow colonization of new biomes. However, because responses to habitat shifts are species specific (Burney and Brumfield, 2009; Cabanne et al., 2016; Porto et al., 2012; Smith et al., 2014), comparative studies are necessary to obtain a full understanding of the evolutionary role of the biogeographic links between Neotropical forests.

4.3. Molecular systematics of Arremon flavirostris and allies

We suggest to split *A. flavirostris* into two full species (*A. flavirostris* and *A. dorbignii*). The current species is divided in two divergent genetic lineages that are completely isolated: subspecies *dorbignii* (central Andes rainforests) and the lineage of *flavirostris*, *devillii* and *polionotus* (Atlantic Forest and gallery forests in the Cerrado and Chaco). These two lineages are morphologically diagnosible (Fig. 2a); i.e. *dorbignii* has longer eyebrow starting at the nape-forehead (not at the upper-eye), a narrower pectoral band (Hellmayr, 1938) and a unique song (Buainain et al., 2016). These two lineages could be considered full species according to different species concepts. For example, according to the phylogenetic concept (Cracraft, 1983), they are full species because represent monophyletic populations (Fig. 5b). Also, according to the general lineage species concept (de Queiroz, 1998), they represent independent evolutionary lineages (i.e., migration between them $M < 1$) that are morphologically diagnosable. Finally, it is not clear if both populations could be separated according to the biological species concept. Even though there is very low gene flow between the Andean and the Atlantic Forest populations, indicating no interbreeding, and they are phenotypically diagnosable (plumage and song), it is impossible to show that both populations would not hybridize if their geographic ranges met (but see Buainain et al., 2016).

Regarding the other subspecies (*flavirostris*, *devillii* and *polionotus*), our analysis did not support them as independent evolutionary entities (Figs. 2 and 5b) (but see Buainain et al., 2016). These subspecies are similar morphologically, with the only difference between them the color of their back plumage (e.g. green in *flavirostris*; grey in *devillii* and *polionotus*) (Hellmayr, 1938; Silva, 1991). However, since they are not genetically divergent (Fig. 5b), we do not suggest considering them as full species. These subspecies of *A. flavirostris* inhabiting the Cerrado and the Atlantic forest present an interesting example of recent evolution of populations, where there is no significant genetic isolation but there is a remarkable phenotypic variation across the region. Perhaps, it would be a product of divergent selection with gene flow across the axis Chaco-Atlantic Forest-Cerrado, where green-backed birds could be positively favored in more humid habitats (i.e., central Atlantic forest and gallery forests in the eastern Cerrado), while grey-backed birds would be favored in drier forests (i.e., eastern Chaco, southern Atlantic forest and western Cerrado). This hypothesis is compatible with the fact that the only other member of *Arremon* with a grey back (*A. abeillei*) also inhabits dry and semideciduous forests. Despite of these subspecies do not represent independent evolutionary lineages, they apparently are a good representation of different ongoing evolutionary phenomena in the group.

Our phylogenetic study also shed light onto the evolutionary identity of *A. franciscanus* (Fig. 5); we showed for the first time *A. franciscanus* is an independent evolutionary lineage. This species inhabits shrubs and arboreal Caatinga in a portion of central Bahia and northern Minas Gerais, Brazil (Ridgely and Tudor, 2009). Their habitat is being degraded and deforested rapidly, and then it is considered near threatened (Rising, 2011). Particularly, *A. fransicanus* plumage resembles *A. semitorquatus* (Raposo, 1997), and up to now there was not any study addressing its genetic identity.

5. Conclusions

We suggest splitting *A. flavirostris* into two full species. The majority of the species shared between the Andean and the Atlantic forests have subspecies that correspond to these regions, most of them not studied from the genetic standpoint. We hypothesize that many of those species will also show a pattern of isolation between forests, a result that would have important consequences for taxonomy and biodiversity conservation.

Our study with *A. flavirostris* supports that the Pleistocene glacial cycles altered ranges of tropical organisms and promoted biogeographic links between forested domains during different climate phases. Our results indicate that the tropical Andes and the Atlantic Forest biodiversity interacted by cycles of connections through a main Cerrado corridor –during glacial maxima–, and perhaps also through a Chaco corridor –during interglacial periods–. These recurrent cycles of connection between the Andean and the Atlantic forests could have been important in the process of avian diversification in the Neotropics.

Acknowledgements

We thank the collectors and staff of the institutions that loaned tissue samples used in this study: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Instituto de Investigación de Recursos Biológicos Alexander von Humboldt; Museu Paraense Emílio Goeldi and Museo de Zoología of the Universidade Federal de Minas Gerais (UFMG). We thank the following institutions for granting collection permits: Administración de Parques Nacionales (Argentina), Ministerio de Ecología de Misiones, and environmental authorities of Bolivia and Brazil. We are also grateful to the Associate Editor Scott Edwards, to two anonymous referees because their comments helped to improve an early version of the manuscript, to Manolo Peres for helps with the ABC analyses, and to Dan Zornizer for the English language collaboration. This study was funded by: the Consejo Nacional de Investigaciones Científicas y Tecnológicas from Argentina (PIP 276, Proyecto Coop. Internacional CNPq-CONICET and CAPES-CONICET, as well as Proyecto Fondo IBOL), the Agencia Nacional de Promoción Científica y Tecnológica from Argentina (PICT 2012 1924 and PICT 2014 2154), and Fundação de Amparo à Pesquisa do Estado de São Paulo (BIOTA, 2013/50297-0) from Brazil, and National Science Foundation (DOB 1343578) and NASA from the USA. This work was partially developed in the Research Center on Biodiversity and Computing (BioComp) of the Universidade de São Paulo (USP), supported by the USP Provost's Office for Research.

Appendix A

See Table A.1.

Table A.1
Samples used for the phylogenetic and phylogeographic analysis of *Arremon flavirostris*. Abbreviations for tissue catalogue ID are: DZ, Departamento de Zoologia, Universidade Federal de Minas Gerais, Brazil; IAvH-CT, Colección de Tejidos Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Colombia; LGEMA, Laboratório de Genética e Evolução Molecular de Aves, Universidad de São Paulo, Brazil; MACN, Bird tissue collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires; MG, Museu Paraense Emílio Goeldi, Belém, Brazil; B, Laboratorio de Biodiversidade e Evolução Molecular, Universidade Federal Minas Gerais, Brazil.

Taxon	Locality number	Locality	Sample size	Tissue ID	Sex	COI	Cyt *b*	FIB5	VLDL9R	G3PDH
Arremon flavirostris dorbignii	1	Paraiso, Chulumani, La Paz, Bolivia (−16.39916667, −67.56055556)	1	MACN 7262	Female	KY940852	KY940919	–	KY941032	KY940981
A. flavirostris dorbignii	2	Pedernal, Provincia Tomina, Dpto. Chuquisaca, Bolivia (−19.36211000, −64.11984000)	4	MACN 6273	Male	KY940853	KY940915	KY940941	KY941033	KY940982
				MACN 6289	Male	KY940856	KY940916	KY940944	KY941036	KY940985
				MACN 6290	Male	KY940855	KY940917	KY940943	KY941035	KY940984
				MACN 6295	Female	KY940854	KY940918	KY940942	KY941034	KY940983
A. flavirostris dorbignii	3	Parque Nacional Calilegua, Mirador de Aguas Negras, Jujuy, Argentina (−23.93330000, −65.22388900)	3	MACN 5628	Female	KY940849	KY940912	KY940938	KY941029	KY940979
				MACN 5677	Female	KY940850	KY940913	KY940939	KY941030	–
				MACN 5697	Male	KY940851	KY940914	KY940940	KY941031	KY940980
A. flavirostris dorbignii	4	2KM E of Ocloya, Jujuy, Argentina (−23.93333333, −65.22388889)	3	MACN 887	Male	FJ027168.1*(Kerr et al., 2009)	KY940909	KY940935	KY941026	KY940976
				MACN 1140	Male	FJ027167.1*(Kerr et al., 2009)	KY940911	KY940936	KY941027	KY940977
				MACN 1143	Male	FJ027165.1*(Kerr et al., 2009)	KY940910	KY940937	KY941028	KY940978
A. flavirostris polionotus	5	Reserva El Bagual, Laishi, Formosa, Argentina (−26.04866000, −58.64393900)	1	MACN 4191	Male	KY940860	KY940926	KY940949	KY941043	KY940991
A. flavirostris polionotus	6	Reserva Natural Educativa Colonia Benítez, Chaco, Argentina. (−27.31805556, −58.94905556)	1	MACN 4188	Female	KY940859	KY940927	–	KY941042	KY940990
A. flavirostris polionotus	7	Parque Nacional Chaco, Chaco, Argentina (−26.80894000, −59.60723000)	3	MACN 4819	Female	KY940861	KY940925	KY940950	KY941044	KY940992
				MACN 4845	Male	KY940862	KY940924	KY940951	KY941045	KY940993
				MACN 4846	Male	KY940863	KY940923	KY940952	KY941046	KY940994
A. flavirostris polionotus	8	EBCO, Corrientes, Argentina (−27.55095000, −58.68441000)	4	MACN 1388	Female	FJ027170.1*(Kerr et al., 2009)	KY940934	KY940945	KY941037	KY940986
				MACN 1678	Female	KY940858	KY940933	KY940948	KY941041	KY940989
				MACN 1700	Male	FJ027169.1*(Kerr et al., 2009)	KY940932	KY940947	KY941039	KY940987
				MACN 2393	Male	FJ027171.1*(Kerr et al., 2009)	KY940931	–	KY941040	KY940988
A. flavirostris polionotus	9	Parque Nacional Mburucuyá, Corrientes, Argentina (−29.00000000, −58.93300000)	3	MACN 5005	Male	KY940864	KY940922	KY940953	KY941047	KY940995
				MACN 5006	Female	KY940865	KY940921	KY940954	KY941048	KY940996
				MACN 5051	Female	KY940866	KY940920	KY940955	KY941049	KY940997
A. flavirostris polionotus	10	Parque Nacional Iguazú, Iguazú, Misiones, Argentina. (−25.67800000, −54.44900000)	2	MACN 2964	Male	FJ027166.1*(Kerr et al., 2009)	KY940930	KY940956	KY941050	–
				MACN 3514	Male	KY940868	KY940929	KY940958	KY941052	–
				MACN 3545	Male	KY940867	KY940928	KY940957	KY941051	KY940998
A. flavirostris devillii	11	Pontal de Paranapanema, Morro do Diabo São Paulo, Brazil (−22.86670000, −52.48330000)	1	LGEMA 1686	Female	KY940857	–	KY940946	KY941038	KY940999

(*continued on next page*)

Table A.1 (*continued*)

Taxon	Locality number	Locality	Sample size	Tissue ID	Sex	COI	Cyt *b*	FIB5	VLDL9R	G3PDH
A. flavirostris devillii	12	Bonito, Mato Grosso do Sul, Brazil (−21.25000000, −56.70000000)	3	MG 51940	Female	KY940891	–	–	KY941073	KY941022
				MG 51941	Male	KY940894	–	KY940975	KY941076	KY941023
				MG 51942	Male	KY940892	–	KY940974	KY941074	KY941024
A. flavirostris devillii	13	Corumbá, Mato Grosso do Sul, Brazil (−19.00874900, −57.67873700)	3	DZ 4570	Female	KY940878	–	–	KY941063	KY941009
				DZ 4571	Male	KY940879	–	KY940969	KY941064	KY941010
				DZ 4778	Male	KY940881	–	–	KY941077	–
A. flavirostris devillii	14	Chapada dos Guimarães, Mato Grosso, Brazil (−13.87174400, −55.68198400)	3	MG 38998	Female	KY940889	–	–	–	KY941020
				MG 38997	Female	KY940888	–	–	KY941072	KY941019
				MG 38999	Male	KY940890	–	–	–	KY941021
A. flavirostris flavirostris	15	Arcos, Minas Gerais, Brazil (−20.26666667, −45.66055556)	4	DZ 4926	Female	KY940882	–	–	KY941066	KY941012
				DZ 4927	Male	KY940883	–	–	KY941067	KY941013
				DZ 4928	Female	KY940884	–	KY940971	KY941068	KY941014
				DZ 4929	Male	KY940885	–	–	KY941069	KY941015
A. flavirostris flavirostris	16	Perdões, Minas Gerais, Brazil (−20.38477900, −45.19987100)	6	DZ 3118	Female	–	–	KY967517	–	KY941016
				DZ 4123	Male	KY940872	–	KY940963	KY941057	KY941004
				DZ 4158	Male	KY940874	–	KY940965	KY941059	–
				DZ 4159	Male	KY940875	–	KY940966	KY941060	KY941006
				DZ 4160	Female	KY940876	–	KY940967	KY941061	KY941007
				DZ 4161	Male	KY940877	–	KY940968	KY941062	KY941008
A. flavirostris flavirostris	17	Itumirim, Minas Gerais, Brazil (−21.23617000, −44.82374700)	1	DZ 4139	Male	KY940873	–	KY940964	KY941058	KY941005
A. flavirostris flavirostris	18	Belo Horizonte, Minas Gerais, Brazil (−19.60256400, −43.98181800)	1	DZ 4617	Male	KY940880	–	KY940970	KY941065	KY941011
A. flavirostris flavirostris	19	Felixlândia, Minas Gerais, Brazil (−18.75003000, −44.91419000)	1	DZ 5014	Male	KY967515	–	–	–	–
A. flavirostris flavirostris	20	Uberlandia, Minas Gerais, Brazil (−18.87770700, −48.33534900)	1	DZ 2356	Male	–	–	KY967516	KY941078	–
A. flavirostris flavirostris	21	Engenheiro Navarro, Minas Gerais, Brazil (−17.27664400, −43.94650100)	2	DZ 5002	Male	KY940886	–	KY940972	KY941070	KY941017
				DZ 5003	Male	KY940887	–	KY940973	KY941071	KY941018
A. flavirostris flavirostris	22	Bocaiúva, Minas Gerais, Brazil (−17.38333000, −43.88333000)	2	B 2254	Male	KY940869	–	KY940959	KY941053	KY941000
				B 2270	Female	KY940870	–	KY940960	KY941054	KY941001
A. flavirostris flavirostris	23	Virgem da Lapa, Minas Gerais, Brazil (−16.78333300, −42.25000000)	2	B 2560	Female	KM896244 (Chaves et al., 2015)	–	KY940961	KY941055	KY941002
				B 3036	Male	KY940871	–	KY940962	KY941056	KY941003
A. flavirostris flavirostris	24	Arinos, Minas Gerais, Brazil (−15.23131400, −46.10474600)	2	MG 41542	Male	–	–	–	KY941079	–
				MG 41543	Male	KY940893	–	–	KY941075	KY941025
A. semitorquatus		Wenceslau Bráz, Paraná, Brazil (−23.86993200, −49.79234600)	1	LGEMA 1350		JN801499.1 (Tavares et al., 2011)	–	–	KY941087	–
A. semitorquatus		Pinhālo, Paraná, Brazil (−23.96666700, −50.05000000)	1	LGEMA 1307	Male	KY940903	–	–	KY941088	–
A. semitorquatus		Simonésia, Minas Gerais, Brazil (−20.11685900, −42.00025700)		B 1422	Female	KY940904	–	–	KY941089	–
A. taciturnus		Lençois, Bahia, Brazil (−12.43277778, −41.36277778)	1	LGEMA 2647		JN801500.1 (Tavares et al., 2011)	–	–	KY941090	–

Table A.1 (*continued*)

Taxon	Locality number	Locality	Sample size	Tissue ID	Sex	COI	Cyt *b*	FIB5	VLDL9R	G3PDH
A. taciturnus		Provincia Caranavi, La Paz, Bolivia (−15.45888889, −67.47833333)	1	MACN 4613	Female	KY940906	–	–	KY941091	–
				MACN 4610	Male	KY940907	–	–	KY941092	–
A. taciturnus		Cumaribo, Vichada, Colombia (4.609166667, −67.86444444)	1	IAvH-CT 8182	Unknown	KY940908	–	–	KY941093	–
A. franciscanus		Caetité, Bahia, Brazil (−14.31527778, −42.56138889)	2	B 4012	Female	KY940895	–	–	KY941080	–
				B 4063	Male	KY940896	–	–	KY941081	–
				B 4064	Female	KY940897	–	–	KY941083	–
A. franciscanus		Campo de Avião, Francisco Sá, Minas Gerais, Brazil (−16.43527778, −43.47083333)	1	LGEMA 13394	Male	KY940898	–	–	KY941082	–
A. schlegeli		Minca, Magdalena, Colombia (11.14263500, −74.11691400)	1	IAvH-CT-09621	Unknown	KY940899	–	–	KY941084	–
A. schlegeli		Reserva Ciudad Antigua, Ciénaga, Magdalena, Colombia (11.00291400, −74.25902600)	1	IAvH-CT-17859	Unknown	KY940900	–	–	KY941085	–
A. schlegeli		Reserva Ciudad Antigua, Ciénaga, Magdalena, Colombia (11.00291400, −74.25902600)	1	IAvH-CT 17863	Unknown	KY940901	–	–	KY941086	–
A. aurantiirostris		Vereda La Miel, Caldas, Colombia (5.65000000, −74.76666667)	1	IAvH-CT 04694	Unknown	KY940848	–	–	–	–
A. aurantiirostris		Bocas Del Toro, Panamá	1			JQ174088.1 (Schindel et al., 2011)	–	–	–	–

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2017.03.025.

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