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Connections between the Atlantic and the Amazonian forest avifaunas represent distinct historical events

Henrique Batalha-Filho · Jon Fjeldså ·
Pierre-Henri Fabre · Cristina Yumi Miyaki

Abstract There is much evidence to support past contact between the Atlantic and the Amazon forests through the South American dry vegetation diagonal, but the spatio-temporal dynamics of this contact still need to be investigated to allow a better understanding of its biogeographic implications for birds. Here, we combined phylogenetic data with distributional data using a supermatrix approach in order to depict the historical connection dynamics between these biomes for New World suboscines. We examined the variation in divergence time and then compared the spatial distributions of taxon pairs representing old and recent divergences. Our results pointed to two distinct spatiotemporal pathways connecting the Atlantic and the Amazonian forests in the past: (1) old connections (middle to late Miocene) through the current southern Cerrado and Mato Grosso and the transition towards the Chaco and palm savannas of Bolivia and Paraguay; (2) young connections (Pliocene to Pleistocene) that possibly occurred through the Cerrado and Caatinga in northeastern Brazil. We suggest that the main events that played important roles in these connections were geotectonic events during the late Tertiary associated with the uplift of the Andes (old connections) and Quaternary climate changes that promoted the expansion of gallery forest through the Cerrado and Caatinga in northeastern Brazil (young connections). Our results provide the first general temporal and spatial model of how the Atlantic and Amazonian forests were connected in the past, which was derived using bird data.

Keywords Neotropical region · New World suboscines · Supermatrix · Worldmap · Biogeography · Miocene · Quaternary

H. Batalha-Filho (✉) · C. Y. Miyaki
Laboratório de Genética e Evolução Molecular de Aves, Departamento de Genética e Biologia Evolutiva, Instituto de Biociências, Universidade de São Paulo, Rua do Matão 277, Cidade Universitária, São Paulo, SP 05508-090, Brazil
e-mail: henrique.batalha@usp.br; rickbio@hotmail.com

J. Fjeldså · P.-H. Fabre
Center for Macroecology, Evolution and Climate at the Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark

Zusammenfassung

Verbindungen zwischen atlantischen und amazonischen Waldvogelfaunen spiegeln distinkte historische Ereignisse wider

Zahlreiche Hinweise belegen ehemalige Kontakte zwischen atlantischen und amazonischen Wäldern über die diagonal durch Südamerika verlaufende Trockenvegetationszone hinweg, allerdings bedarf die raumzeitliche Dynamik dieser Kontakte noch näherer Untersuchung, um deren biogeografische Auswirkungen auf Vögel besser verstehen zu können. Hier fassten wir phylogenetische Daten mit Verbreitungsdaten in einer Supermatrix-Analyse zusammen, um so die Dynamik der historischen Verbindungen zwischen diesen Biomen für Neuwelt-Suboscine abzubilden. Wir untersuchten die Variation im Zeitpunkt der Artentrennung und verglichen dann die räumliche Verteilung von Taxonpaaren, die alte und rezente Trennungsereignisse repräsentieren. Unsere Ergebnisse deuten auf zwei distinkte raumzeitliche Verbindungswege zwischen

atlantischen und amazonischen Wäldern in der Vergangenheit hin: (1) alte Verbindungen (Mittleres bis Oberes Miozän) durch den heutigen südlichen Cerrado und Mato Grosso sowie den Übergang zum Chaco und den Palmsavannen Boliviens und Perus; (2) junge Verbindungen (Pliozän bis Pleistozän), möglicherweise durch die Cerrados und die Caatinga im nordöstlichen Brasilien. Unserer Ansicht nach spielten die folgenden Hauptereignisse eine wichtige Rolle für diese Verbindungswege: geotektonische Ereignisse während des späten Tertiärs im Zusammenhang mit der Auffaltung der Anden (alte Verbindungen) sowie Klimaänderungen im Quartär, die die Ausbreitung von Galeriewäldern durch Cerrado und Caatinga im nordöstlichen Brasilien begünstigten (junge Verbindungen). Auf der Grundlage von Vogeldaten stellen unsere Ergebnisse die erste allgemeine Näherung für Zeiträume und die Art und Weise dar, wie atlantische und amazonische Wälder in der Vergangenheit in Verbindung standen.

Introduction

It is well known that many sister species and lineages are disjunctly distributed in the Brazilian Atlantic Forest (AF) and in the Amazon Basin (AM), but this biogeographic pattern has never been explored in depth for birds. The two biomes are separated by a broad diagonal of more xeric habitats comprising the Chaco, the Cerrado uplands, and the Caatinga (Ab'Saber 1977), and together they encompass one of the most diverse tropical forests of the world. There is much evidence to support past contact between the AF and the AM through this dry vegetation diagonal (Auler et al. 2004; Auler and Smart 2001; Behling et al. 2000; Costa 2003; Oliveira et al. 1999; Patton et al. 1997; Patton and Costa 1999; Vilela et al. 2009; Por 1992; Wang et al. 2004; Willis 1992). Palynological and geological data from these studies cover the late Pleistocene (the last 0.9 mya) and indicate that there were wetter periods that allowed the expansion of gallery forest into the Cerrado and Caatinga, providing connections between the AF and the AM (Auler et al. 2004; Auler and Smart 2001; Behling et al. 2000; Oliveira et al. 1999; Wang et al. 2004). Costa (2003) compared the phylogeographic patterns of small mammals in the AF and the AM and found lineages from either the AF or the AM in the Cerrado. Costa (2003) also observed that some taxa from northern AF are more closely related to AM taxa than to southern AF forms. Silva (1996) showed that several birds from the AM and the AF show distributions that extend along the Cerrado gallery forests. However, there are several species with disjunct distributions in these forested biomes (e.g., see Ridgely and Tudor 1994 for birds; see Vivo 1997 for mammals; see Martini

et al. 2007 for plants), and this reinforces the idea that the dry vegetation diagonal plays an important role in the connection of theses biomes. Similarly, there is evidence from Africa supporting episodes of faunal connection across the "arid corridor" in eastern Africa between the main rainforest tracts and those near the Indian Ocean (the African Rift; Couvreur et al. 2008; Tolley et al. 2011). However, questions concerning the timing and nature of this connection are still to be conclusively answered. Such questions include: were the AF and AM biota connected just once in the past? Was the connection related solely to Quaternary climate changes? If not, when did this (these) connection(s) occur? Were there different pathways connecting AM and AF?

Possible explanations for the observed patterns could be extinction, dispersal, or vicariance (Crisci et al. 2003). A basic assumption of vicariance biogeography (as well as panbiogeography) is that generalized patterns can be detected by searching for concordance in area cladograms (or tracks) across multiple lineages. Although there are numerous known cases of different historical events generating similar patterns (e.g., Tuomisto 2007), there is still a widespread tendency to treat similar patterns as indications of common biogeographic events. Besides, distinct co-distributed taxa could present similar cladogenetic splits if speciation and/or diversification are driven by vicariance, as the distributions of the ancestor populations would have been affected in a similar way when the barriers to dispersal formed.

However, it is important to distinguish true congruence, where the taxa and areas share the same history (Cracraft 1985, 1988) from "pseudocongruence" (Cunningham and Collins 1994; Donoghue and Moore 2003), where cyclical processes (such as orbitally driven climatic/vegetational changes; Bennett 1990; Hooghiemstra et al. 1993) result in the repetition of historical events. This could be a repeated process of range expansion and retreat. We also need to consider whether entirely different biogeographic events, superimposed over millions of years, may in some cases result in patterns that we perceive as being congruent.

Recently, the integration of distributional and phylogenetic data has given robust insights into diversification processes and biogeographical patterns of tropical forests (Fjeldså et al. 2007; Fjeldså and Irestedt 2009; Fjeldså and Rahbek 2006; Roncal et al. 2011). This kind of approach connects ecological and historical biogeographies and gives insight into community assembly and species richness patterns by considering the biogeographical history of the species and clades that make up these patterns (Wiens and Donoghue 2004).

In the work described in this paper, we applied this approach to New World suboscine birds, a monophyletic group (Barker et al. 2004) with 1,200 extant species. This

group evolved within South America, but some subclades recently expanded to colonize Central and North America during the great American exchange (Smith and Klicka 2010; Weir et al. 2009). Several phylogenies for this group have been published (Derryberry et al. 2011; Irestedt et al. 2002, 2004, 2009; Moyle et al. 2009; Ohlson et al. 2008; Tello et al. 2009), which provide a large data source for biogeographic inferences.

In this paper, taxa with disjunct Amazonian/Atlantic forest distributions were examined to investigate whether such disjunctions are the result of a single (or at the very least a recurrent) range fragmentation event or entirely different events. This was done in two steps: first by examining the degree of genetic divergence between them, and second by examining their geographical distributions.

Thus, we aimed to combine phylogenetic data using a dated phylogeny with distributional data in order to try to depict the historical connection dynamics between AF and AM. We examined the variation in divergence time and then compared spatial distributions of taxon pairs representing old and recent divergences. This allowed us to address two main questions. (1) When and where did this (these) connection(s) happen? (2) Which historical events were responsible for the interchange of avifauna between the AF and the AM?

Materials and methods

Taxa selection and phylogenetic analyses

The first step was to identify sister groups (species or lineages) with disjunct distributions in the AF and the AM. This was done by performing a comprehensive search of the *Handbook of the Birds of the World* (del Hoyo et al. 2003, 2004), and utilizing information on species and population distributions as well as their putative evolutionary relationships with published phylogenetic information (Derryberry et al. 2011; Irestedt et al. 2002, 2004, 2009; Moyle et al. 2009; Ohlson et al. 2008; Tello et al. 2009). Thus, we selected only pairs of sister taxa with AF and AM distributions that had a well-supported phylogenetic grouping (including cases where an AF species is sister to a small group of species with an AM distribution). We also included, as recent splits, disjunctly distributed species whose populations in the AF and the AM are slightly differentiated morphologically, suggesting a recent (Plio-Pleistocene) split (see below). Unfortunately, no DNA sequence data on these populations are available, and we acknowledge that it would be desirable to use such data to estimate their divergence times. However, we decided to include these groups in our analyses with the assumption

that the current species-level taxonomy reflects relationships accurately. While there may be some exceptions where subspecies in the AM and the AF are genetically more divergent than their subtle morphological differences would suggest, but we find it unlikely that such divergences would be older than the 5.5 million years (Plio-Pleistocene period) that we regarded here as a recent split.

Other New World subsoscine species were also included to help strengthen the support for some phylogenetic relationships (see Table S1 of the Electronic supplementary material, ESM). Based on Barker et al. (2004), the outgroups used were: *Pitta baudii*, *Smithornis rufolateralis*, *Corvus corone*, *Parula americana*, *Menura novaehollandiae*, *Acanthisitta chloris*, and *Pterocles namaqua* (Table S1 of the ESM).

The sequences of six genes for which data are available for many species of New World subsocines were downloaded from the GenBank/EMBI databases: one mitochondrial—cytb; three nuclear introns—myo2, G3PDH and FIB5; and two nuclear exons—RAG-1 and RAG-2 (Table S1 of the ESM). Thus, we selected 83 species (including outgroups) to reconstruct the phylogenetic relationships of New World subsocines from the AF and the AM (Table S1 of the ESM). Sequences were aligned using MUSCLE (Edgar 2004) in MEGA5 (Tamura et al. 2011). All alignments were inspected and corrected manually when necessary. The genes were concatenated using SeaView4 (Gouy et al. 2010), and this alignment contained 7,092 characters (the percentage of the data that are missing for each gene is shown in Table S2 of the ESM).

The best-fit substitution model for each partition was estimated using MrModeltest 2.2 (Nylander 2004) based on Akaike's information criterion (AIC). We used Bayesian and maximum likelihood inferences based on six partitions (Table S2 of the ESM) to reconstruct phylogenies using MrBayes 3.1.2 (Huelsenbech and Ronquist 2001) and RAxML (Stamatakis et al. 2008), respectively. Bayesian runs consisted of 17 million generations of two independent runs with four chains of Markov chain Monte Carlo (MCMC) each. The first one million generations were discarded as "burn-in," and the trees were sampled every 500 generations. The burn-in and convergence diagnostics were estimated using the PSRF (potential scale reduction factor), where values close to one indicate a good convergence between runs (Gelman and Rubin 1992). We also assessed the chain convergence by checking the posterior distribution plots of each run using Tracer 1.5 (http://beast.bio.ed.ac.uk/Tracer), verifying that the ESS values were >200. We carried out RAxML analysis in the CIPRES Science Gateway (Miller et al. 2010) using the same partitions of Bayesian inference under the GTRAC model; invariable sites and the gamma distribution were estimated

for each partition during the run. Node supports for the maximum likelihood analyses were estimated by performing 100 bootstrap replications.

Date estimates were obtained by implementing a Bayesian relaxed clock model in BEAST 1.6.1 (Drummond et al. 2006; Drummond and Rambaut 2007) based on the concatenated dataset. Two independent runs with 50 millions of generations were obtained using the following parameters: the Yule prior, a random starting tree, the GTR+I+Γ model, parameters sampled every 1,000 steps, a burn-in of 10 %, and an assumption of an uncorrelated relaxed lognormal clock. We used the geological split between New Zealand and Antarctica as the calibration point, as this has been related to the basal separation of the *Acanthisitta* lineage from the other passerines (Barker et al. 2002, 2004; Ericson et al. 2002). Thus, we used a normally distributed tree prior with a mean of 78 mya and a standard deviation of 7, as used by Irestedt et al. (2009). To check the convergence of the parameters between runs, we used Tracer 1.5, verifying that the ESS values were >200. The consensus topology with the divergence times was visualized in FigTree 1.3.1 (http://tree.bio.ed.ac.uk/software/figtree).

Distributional analysis

We used the bird distribution for South America that is digitalized in Worldmap (Williams 1998), which was generated from a comprehensive global distribution database developed at the Center for Macroecology, Evolution and Climate (January 2011 version). The resolution of the map used was $1° \times 1°$ quadrates (latitude × longitude), following the approach outlined in Brooks et al. (2001) and in Rahbek and Graves (2001). Maps represent a conservative source of extent-of-occurrence for the breeding ranges based on museum specimens, published sighting records, and spatial distribution of habitats of documented records (>1,000 references used), and have been validated by many experts.

To estimate the possible different pathways of contact between the AF and the AM, we selected species from the young and old divergences based on Bayesian dating. Ranges of young and old divergences assumed here were: young—comprising divergence during the Pliocene and Pleistocene (the last 5.5 million years); old—comprising the Miocene period (ranging from 5.6 to 23 million years ago). Thus, we generated species richness maps for young and old divergences.

In order to assess the degree of co-distribution between the richness maps of young and old splits, we applied a correlation test (rho, ρ) between the maps, and this was visualized by overlaying a two-color scheme on the species distribution (Williams and Gaston 1998).

Results

Phylogenetic reconstruction and dating

Our supermatrix consisted of 7,092 characters and provided a robust dataset to estimate the phylogenetic relationships and to date New World subsoscines divergencies. The best-fit model estimated for each gene partition as well as the length of each gene are shown in Table S2 of the ESM. The phylogenetic reconstruction inferred by the Bayesian and maximum likelihood (Fig. S1 of the ESM) approaches were congruent and agreed with previous published phylogenies (Irestedt et al. 2002, 2004, 2009; Moyle et al. 2009; Ohlson et al. 2008; Tello et al. 2009). All splits between the AF and the AM identified based on the supermatrix topologies showed strong node support values.

The dated chronogram generated by BEAST revealed that the majority of the splits between pairs of sister groups investigated here occurred before the Plio-Pleistocene (Fig. S2 of the ESM). The only exceptions were the younger splits: *Mionectes rufiventris* versus *M. oleagineus* and *M. macconnelli* (4.85 mya); *Chiroxiphia caudata* versus *C. boliviana* (4.17 mya); and *Dendrocolaptes platyrostris* versus *D. picumnus* (4.2 mya). In addition, it was possible to identify very old splits, such as *Piprites pileata* versus *P. chloris* (25.76 mya) and *Psilorhamphus guttatus* versus *Liosceles thoracicus* (21.63 mya).

Species included in our Worldmap analyses that showed young divergences provided a good aid to understanding the dynamics of past connections between the AF and the AM, since no sequences are available for most of these populations in GenBank. Furthermore, phylogeographic studies of bird species distributed disjunctly in these biomes suggested divergence in the Pleistocene (Marks et al. 2002; Miller et al. 2008; Nyári 2007).

Spatiotemporal patterns

We selected a total of 33 and 29 taxa to build the richness maps for young and old splits, respectively (Table S3 of the ESM). These taxon pairs represent 32 young and 10 old splits between the AF and the AM (Fig. S2 and Table S3 of the ESM). The few species that were used in the dating analyses but not included in richness maps exhibited uncertain sister species relationships between the AF and the AM or low node support in the phylogenetic reconstruction.

The overall species richness maps for old and young splits showed a disparity in the AF taxa distribution (Fig. 1). Interestingly, nearly all AF species that originated from old splits occur in central and southern AF (Fig. 1a), whereas taxa that originated from recent splits occur
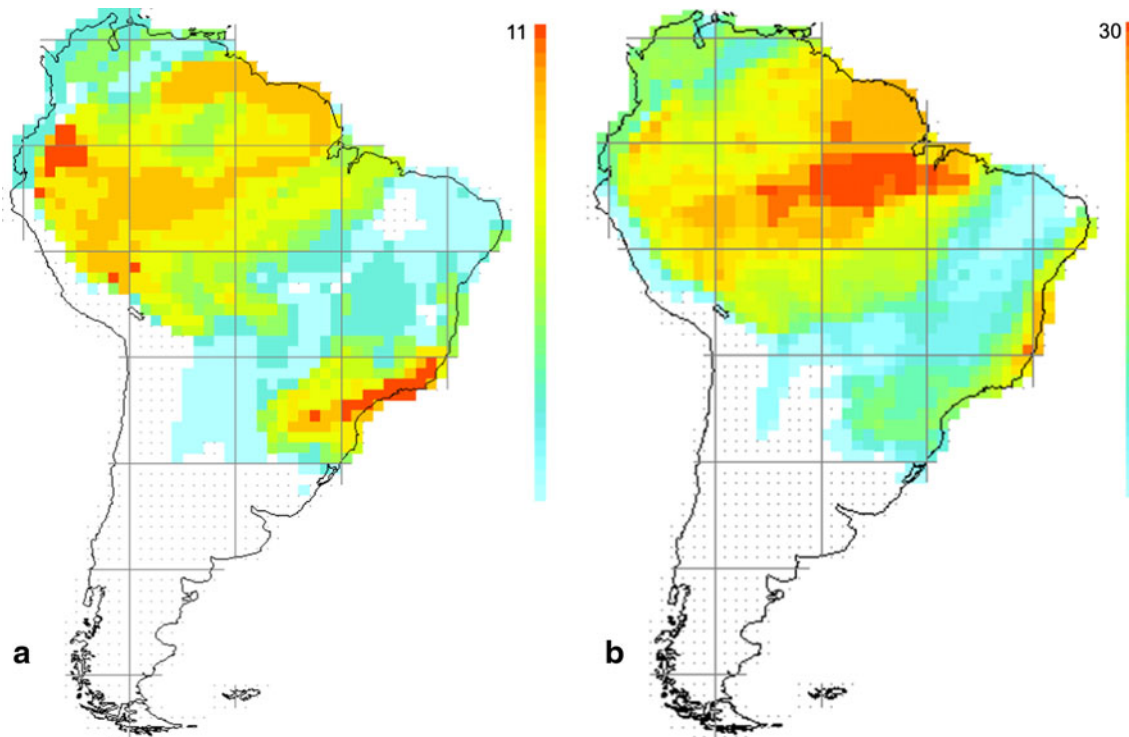
Fig. 1 Species richness variation maps of New World suboscines for disjunctions between the Atlantic Forest and the Amazon Basin. **a** Geographical distribution of 21 taxon pairs representing old divergences (Miocene: 5.6–23 mya) between these biomes.

b Geographical distribution of 37 taxon pairs representing young divergences (Plio-Pleistocene: the last 5.5 mya) between these biomes. *Bars* in both maps indicate the species richness for each pixel

predominantly in northern AF (Fig. 1b). Also, there is a contrast between the distributions of old and young taxa in the AM. Old taxa are mainly found in the western part of the basin and in the Guianas, and in a rather restricted area along the lower Amazon. In contrast, taxa representing younger splits are predominantly present in the lower AM at the north of Pará and in the eastern Amazonian states of Brazil (Fig. 1b). The correlation between maps was moderate ($\rho = 0.78$), but the two-color map shows a clear distinction in the distributions of young and old splits of AF taxa (Fig. 2). However, more green (young splits) is evident for the Caatinga and northern Cerrado, whereas there is a predominance of blue in southern Cerrado as well as in northern Chaco (Fig. 2).

A large number of old AF species, mostly from the cooler southern uplands, have corresponding sister species in the tropical Andes, mainly in Bolivia and Peru (not shown), and some species have disjunct populations in the Andes and the AF (see Ridgely and Tudor 1994). Therefore, these biomes may have been connected by two spatiotemporally distinct pathways, as observed here for the AF and the AM. Percequillo et al. (2011) also suggested a close relationship historically between the AF and the Andes for mammals.

Discussion

In this study, the use of a dated avian molecular phylogeny in combination with distributional data provided an evolutionary time perspective on the dynamics of historical connections between the AF and the AM. In concordance with previous studies, we found three putative pathways connecting the AF and the AM (Auler et al. 2004; Costa 2003; Oliveira et al. 1999; Por 1992; Wang et al. 2004). To our knowledge, this is the first study to present a general spatiotemporal model for the biogeographical connections between the two forest biomes based on bird data (Figs. 2, 3).

Our data show that the Quaternary climatic changes were important in the interchange of avifauna between these two biomes, and that geological events during the Miocene, such as Andean uplift (Hoorn et al. 2010) and associated changes in the axial grove to the east—the establishment of broad foreland basins and marine incursions (Cozzuol 1996; Haq et al. 1987; Paxton and Crampton 1996; Räsänen et al. 1995; Wesselingh et al. 2006; Wesselingh and Salo 2006), may also have played significant roles (see below). Cracraft (1985), in his definition of areas of avian endemism in South America, postulated that these areas are primarily historical
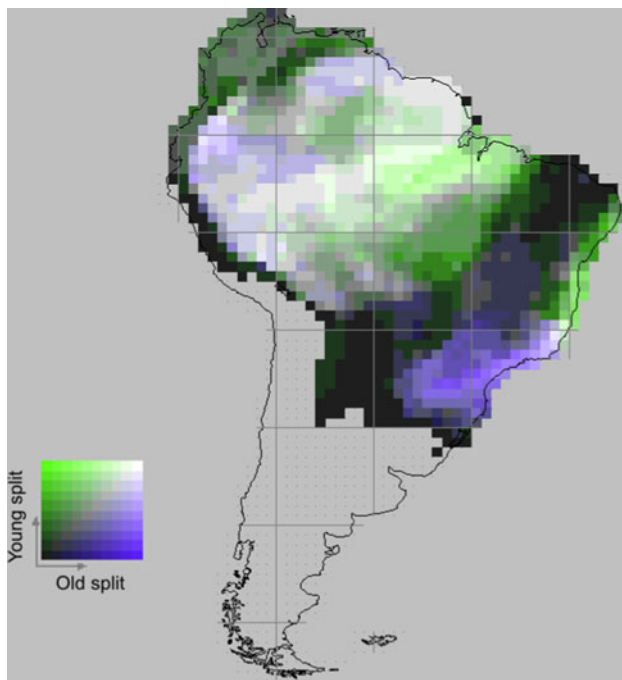
Fig. 2 Correlation map comparing geographic distributions for taxon pairs comprising old and young divergences, $\rho = 0.78$. The colors show the level of overlap: *green shades* represent young splits, *blue shades* represent old splits, and *white* represents completely overlapping distributions (color figure online)

entities rather than simply manifestations of a single, coherent ecology or consequences of climatic–vegetational changes during the Pleistocene. Fjeldså (1994) postulated that massive radiations of South American terrestrial biota occurred during the upper Tertiary, but Rull (2008) and Derryberry et al. (2011) documented a continuous rate of diversification during the Neogene.

In our study, species richness maps show clearly early and late AM/AF disjunctions. These events seem to represent the signatures of at least two distinct biogeographic connections (Figs. 1, 2): (1) the old connections (middle to late Miocene) between these two biomes appear to have existed along the southern margin of the modern Cerrado and in Mato Grosso, or on the transition towards the Chaco and palm savannas of Bolivia and Paraguay (Fig. 3); (2) the young connections (Pliocene to Pleistocene) possibly occurred through the Cerrado and Caatinga in northeastern Brazil (Fig. 3). Furthermore, there seem to be differences in the spatial occupations of young and old divergences within the AF, with the old ones restricted to the southern AF, upland forests at southern Bahia, Minas Gerais, Espírito Santo, Rio Janeiro, and northern São Paulo, and lowland forests in the south, while taxa representing young AF/AM divergences occur in lowland coastal forests from northern Rio de Janeiro to northeastern Brazil (Figs. 1, 2). This pattern also involves two climatic settings, as forests in southern Brazil are cooler than lowland forests in the

northern part of the AF. However, most of the species of the upland forests of southern Brazil have their nearest relatives in the Andes, as the bending of the Bolivian oroclin (Chapare Buttress) made contact with the Brazilian Shield up until the Plio-Pleistocene, when the continuous crust thickening in the Bolivian Andes caused geological subsidence and the formation of hydrologically unstable savannah plains that now form a barrier between the Andean and South Brazilian forest faunas (Hanagarth 1993; Silva 1994).

The old pathway connecting the AF and the AM

Based on the species richness map comprising old divergences between the AF and the AM (Figs. 1a, 2), we hypothesize that an old pathway connected these biomes during much of the Miocene along the western edge of the Brazilian cratonic shield, from the northern modern Chaco in the state of Mato Grosso in Brazil, west to Bolivia and Paraguay, and from the state of Rondônia southeast to the state of Paraná (Brazil) (Fig. 3). During the Miocene, the axial grove of the western Amazon Basin expanded to become broad foreland basins characterized by marine and fresh water flux (7–23 mya; see Hoorn et al. 2010; Hoorn and Wesselingh 2010; Lundberg et al. 1998; Wesselingh et al. 2006; Wesselingh and Salo 2006), and there was also a shift in the position of the watershed between the Amazon and the Paraná Sea (Lundberg et al. 1998; Marshall et al. 1993; Marshall and Lundberg 1996; Roddaz et al. 2006). Despite controversies, these paleoseas could have been connected during the late Miocene through the Bolivian/Paraguayan Chaco (Hulka et al. 2006; Roddaz et al. 2006). In these scenarios, we can hypothesize that a pathway may have connected the AF and the AM along these paleoseas and the Chapare Buttress (Lundberg et al. 1998; Roddaz et al. 2006). This pathway could have originated via elevated channel belts (late Tertiary) through flooded savannas that may have provided dispersal pathways for terrestrial organisms (Wesselingh and Salo 2006). Besides, it is well known that the Andean uplift was crucial for the evolution of Amazonian landscapes (Hoorn et al. 2010; Hoorn and Wesselingh 2010), and played a key role in the diversification of organisms in adjacent regions. Also, molecular studies on mammals (Galewski et al. 2005) and lizards (Pellegrino et al. 2011) have postulated old connections (Miocene) between the AF and the AM.

All 19 lineages of New World suboscines that diverged in the mid-Oligocene are present in the AF (data not shown). This observation raises the possibility that many New World suboscine relict lineages originated within the AF, and that only during the Miocene did they colonize the AM. Also, Irestedt et al. (2002) suggested that tracheophone birds originated in southern AF.
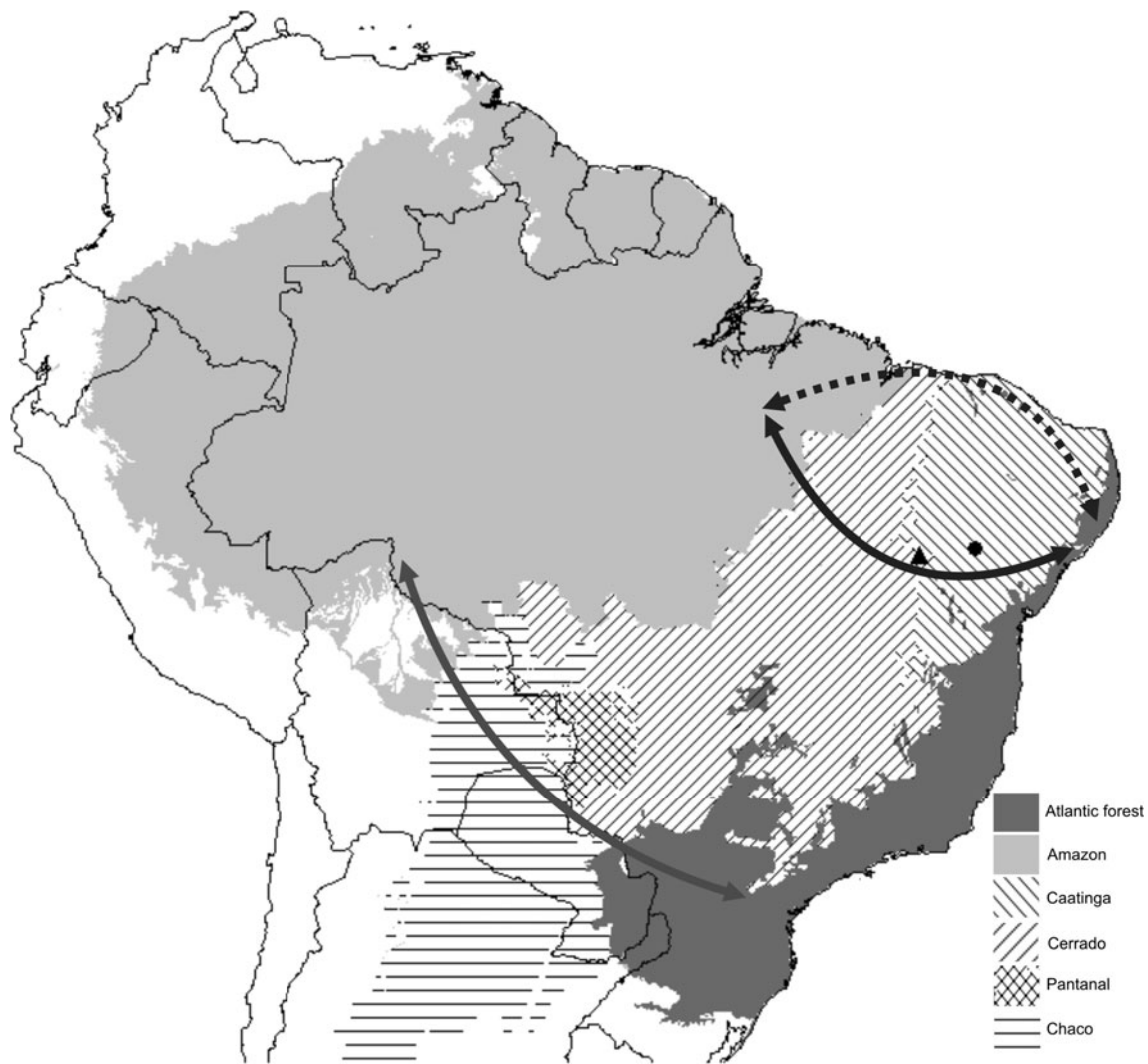
Fig. 3 Representation of the hypothetical historical pathways connecting the Atlantic Forest and the Amazon Basin. *Double headed arrows* represent pathways. The *dark gray arrow* corresponds to old contacts, whereas the *black arrows* correspond to young contacts. The *broken black arrow* shows a less commonly observed young pathway, while the *continuous black arrow* represents a more commonly observed young pathway (see text for more details). These pathways are supported by other studies that are not based on bird data: Andrade-Lima (1982), Auler et al. (2004), Costa (2003), Oliveira et al. (1999), Por (1992), and Wang et al. (2004). The dots in the Caatinga are localities in which there is evidence of the presence of gallery forest during the late Pleistocene (>0.9 mya), based on paleopalynological and speleothems (*triangle* Oliveira et al. 1999; *circle* Auler and Smart 2001 and Wang et al. 2004)

Furthermore, Por (1992) suggested a pathway connecting the AF and the AM through the Paraná River basin, and this is in accordance with our hypothesis. Costa (2003) also showed that this route could have been important for small mammals.

Young pathways connecting the AF and the AM

Our analyses suggest the presence of young pathways connecting the AF and the AM through current distributions in northern Cerrado and Caatinga (Fig. 3). Based on previous evidence (Auler et al. 2004; Costa 2003; Oliveira et al. 1999; Por 1992; Wang et al. 2004), we can also suggest two connection pathways in northeastern Brazil: one through the coastal zones of Maranhão, Piauí, Ceará, and Rio Grande do Norte (Brazil), and another through Tocantins and Bahia (Brazil; Fig. 3).

The most northern young pathway is congruent with the presence of the "Brejos de Altitude" in this area. These "brejos" are relict rain forests enclaved in the Caatinga, and they represent current forest refuges (Andrade-Lima 1982). However, this pathway possibly played a minor role in the young AF/AM connections, as most of the birds with disjunct distributions between the AF and the AM included in our study do not occur in these areas in the state of Ceará. Albano and Girão (2008)

and Girão et al. ([2007](#)) only registered *Xiphorhyncus guttatus*, *Dendrocolaptes platyrostris*, *Rhynchocyclus olivaceus*, *Capsiempis flaveola*, *Attila spadiceus*, *Myrmotherula axillaris*, and *Xenops minutus* in these areas. In addition, Cavalcanti and Tabarelli ([2004](#)) showed that "brejos" and lowland Atlantic forest from northeastern Brazil are distinct phytogeographical units. Nevertheless, it is conceivable that these "brejos" intermittently constituted suitable habitats during the Plio-Pleistocene for most species with AF/AM disjunctions, which have since gone extinct in these areas.

Some Plio-Pleistocene connections may have also existed further south during contractions and retractions of gallery forests during the Quaternary climate episodes. Such pathways are supported by paleopalynological and geological studies (Auler et al. [2004](#); Auler and Smart [2001](#); Oliveira et al. [1999](#); Wang et al. [2004](#)) indicating the presence of gallery forest in the Caatinga in Bahia (Brazil) during the late Pleistocene (>0.9 mya; Fig. [3](#)).

There are few molecular studies on the AF/AM disjunction, but their results are in accordance with the data shown here. Costa ([2003](#)) pointed out that some small mammals that occur in the AF and the AM diverged during the Pleistocene. Also, Cabanne et al. ([2008](#)) and Weir and Price ([2011](#)) suggested that woodcreepers species endemic to the AF diverged from its Amazonian sister species or group during the Pliocene ($\cong 3$ mya), and that the connection between these biomes possibly occurred through northeastern Brazil. However, Martins et al. ([2009](#)) observed that AF/AM populations of a vampire bat diverged in the Pleistocene, following the expansion of dry habitats between these two biomes.

These results have allowed us to propose the first general temporal and spatial model of the historical connections between the AF and the AM. Future historical demographic and phylogeographic studies of organisms with disjunct distributions in these biomes would provide fine-scale tests of this model, and uncover further complexities regarding the nature of the biogeographic connections between the two biomes that are not readily apparent in our study.

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