Divide to conquer: a complex pattern of biodiversity depicted by vertebrate components in the Brazilian Atlantic Forest

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The identification of northern and southern components in different vertebrate species led researchers to accept a two-component hypothesis for the Brazilian Atlantic forest (BAF). Nevertheless, neither a formal proposal nor a meta-analysis to confirm this coincidence was ever made. Our main objective here was therefore to systematically test in how many vertebrate components the BAF could be divided by analysing existing empirical data. We used two approaches: (1) mapping and comparing the proposed areas of vertebrate endemism in the BAF and (2) analysing studies mentioning spatial subdivisions in distinct forest-dependent vertebrates within the biome, by the use of panbiogeography. The four large-scale endemism area components together with the six small-scale panbiogeographical ones allowed the definition of three BAF greater regions, subdivided into nine vertebrate components, latitudinally and longitudinally organized. Empirical time estimates of the diversification events within the BAF were also reviewed. Diversification of these vertebrates occurred not only in the Pleistocene but also throughout the Miocene. Our results confirm the BAF's complex history, both in space and time. We propose that future research should be small-scale and focused in the vertebrate components identified herein. Given the BAF's heterogeneity, studying via sections will be much more useful in identifying the BAF's historical biogeography. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **107**, 39–55.

ADDITIONAL KEYWORDS: biotic components – Brazilian Atlantic forest – distribution patterns – endemism areas – heterogeneous biome – panbiogeography – vertebrates.

INTRODUCTION

The Brazilian Atlantic forest (BAF) is considered the most threatened biodiversity hotspot in South America (Myers *et al.*, 2000). The demand for agricultural land and cattle farms, and the rapid expansion of urban areas are amongst the major threats (Conservation International do Brasil *et al.*, 2000). Nevertheless, the last estimates for the BAF biodiversity account approximately 20 000 vascular plant species and over 2300 vertebrate species, half of the latter being endemic and about 150 with threatened status (Conservation International do Brasil *et al.*, 2000). This biome includes all forest physiognomies from north-eastern Brazil to its south, including coastal Atlantic rain forests, semi-deciduous forests, subtropical *Araucaria* (Jussieu) forests and *brejo* forests (Oliveira-Filho & Fontes, 2000; Fig. 1A).

In the last decade, interest in clarifying the origin of the BAF biodiversity has increased. The refugia hypothesis has been fully proposed and tested (Carnaval & Moritz, 2008), but has proved to be
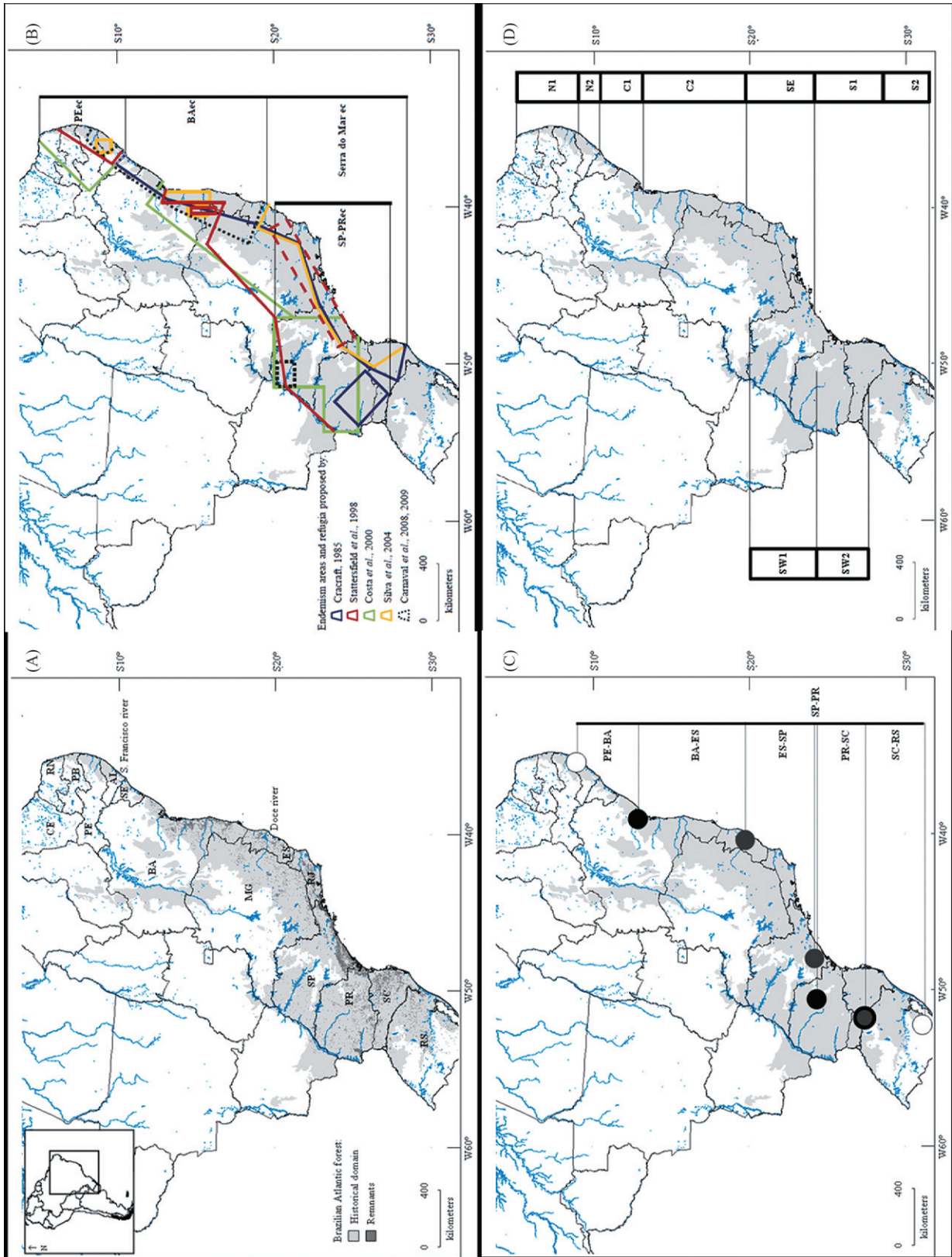
Figure 1. The Brazilian Atlantic forest (BAF) and the vertebrate components. A, BAF extension (CSR, 2007) and the location of the federal states mentioned in the text. B, geographical representation of the endemism areas and refugia proposed so far and their four most consensual biotic components, named after the literature: Pernambuco endemism component (PEec), Bahia endemism component (BAec), Serra do Mar endemism component (Serra do Mar ec), and São Paulo-Paraná endemism component (SP-PRec). C, convergence zones (nodes) found by the panbiogeographical analysis and their respective six biotic components. Convergence zones (nodes) were characterized by the convergence of two and three (white, PE and RS, respectively), four (black with grey, SC), six (grey, ES and SP) and more than ten (black, BA and PR) generalized tracks. D, our nine BAF vertebrate components, named with reference to their location. C2 (Centre 2) is coincident between endemism areas and panbiogeographical analyses. N1 (North 1), SW1 (Southwest 1) and S2 (South 2) are corroborated only by one analysis. All the others are supported by both analyses, at least to some extent. N, North; C, Centre; S, South; SE, Southeast; SW, Southwest. Abbreviations for Brazilian federal states (convergence zones and vertebrate components named thereafter): CE, Ceará; RN, Rio Grande do Norte; PB, Paraíba; PE, Pernambuco; AL, Alagoas; SE, Sergipe; BA, Bahia; MG, Minas Gerais; ES, Espírito Santo; RJ, Rio de Janeiro; SP, São Paulo; PR, Paraná; SC, Santa Catarina; RS, Rio Grande do Sul.

insufficient to explain the diversification of the vertebrates (Martins, 2011). By contrast, the spatial organization of vertebrate diversity within and between taxa has been investigated by several studies, based both on molecular and on morphological data (e.g. Ditchfield, 2000; Costa, 2003; Lessa, Cook & Patton, 2003; Faivovich *et al.*, 2004; Carnaval *et al.*, 2009). Consequently, different areas of vertebrate endemism were proposed within the BAF (Cracraft, 1985; Costa *et al.*, 2000; Silva, Sousa & Castelletti, 2004), and phylogeographical studies have shown the existence of distinct southern and northern clades in several vertebrate taxa (e.g. Puorto *et al.*, 2001; Pellegrino *et al.*, 2005; Grazziotin *et al.*, 2006; Moraes-Barros *et al.*, 2006; Martins *et al.*, 2007). These findings resulted in a generally accepted hypothesis that the BAF comprises two latitudinal components of diversity (Costa, 2003; Moraes-Barros *et al.*, 2006; Carnaval & Moritz, 2008; Lara-Ruiz, Chiarello & Santos, 2008). Even so, the geographical coincidence amongst all northern and southern vertebrate components and its relationship to the areas of endemism described was not tested. In fact, no formalization of the two-component hypothesis was ever made. The complexity of the BAF's biogeographical history is not a new idea (Cracraft & Prum, 1988; Costa, 2003), and recent studies point to a more intricate scenario regarding vertebrate structure (e.g. Brunes *et al.*, 2010; Thomé *et al.*, 2010; D'Horta *et al.*, 2011).

Here we aimed to test the two-component hypothesis through the use of panbiogeography. Panbiogeography is used to describe the distribution patterns of taxa (Croizat, 1952), and it has been recently used in the study of invertebrates (Nihei & Carvalho, 2005; Löwenberg-Neto & Carvalho, 2009), plants (Heads, 2008) and vertebrates (Arzamendia & Giraudo, 2009). It can also be applied in evolution (Grehan & Schwartz, 2009) and conservation (Prevedello & Carvalho, 2006) studies, and in the description of a biome's biotic components, together with analysis of its areas of endemism (Morrone, 2009).

We therefore conducted a survey of the literature on vertebrate species distribution in the BAF focusing on: (1) summarizing vertebrate areas of endemism in the BAF, and (2) analysing the geographical coincidence of vertebrate diversity patterns described within the BAF. We also provide a comparative and integrative discussion focusing on patterns rather than processes and in light of our results and other biogeographical data.

METHODS

The ISI Web of Knowledge and the Google Scholar online databases of published studies were used to find studies mentioning a spatial differentiation in

studies of the distribution and areas of vertebrate endemism in the BAF. The search was performed using mixed expressions including 'Brazilian Atlantic forest', 'endemism area', 'South America', 'vertebrates', and 'Brazil', and encompassed articles published until 31 August 2011. References in these publications were also checked.

As we intended to study the BAF we have only selected forest-dependent taxa (Porzecanski & Cracraft, 2005). We focused our analysis on the study of vertebrates. Furthermore, we used the BAF definition of Oliveira-Filho & Fontes (2000), so we excluded localities within gallery forests, although both forest types can be related (Costa, 2003; Fernandes, Franco & Fernandes, 2004).

With regard to the first issue, i.e. to summarize the BAF areas of vertebrate endemism, the program DIVA-GIS version 7.1.7.2 and its draw shape tool (Hijmans *et al*., 2005) were used to map and represent the areas of endemism.

Secondly, we intended to test whether the BAF can be divided in the two northern and southern vertebrate components as recognized by researchers (e.g. Costa, 2003; Moraes-Barros *et al*., 2006; Carnaval & Moritz, 2008; Lara-Ruiz *et al*., 2008). This was assessed and graphically represented using the panbiogeographical algorithm implemented in Martitracks (Echeverría-Londoño & Miranda-Esquivel, 2011).

To describe the BAF vertebrate components, we compared the resulting panbiogeographical pattern with that observed in the endemism area analysis.

distributions within the BAF were considered, defined by the use of either molecular or morphological markers. Likewise, we considered both BAF endemics and non-endemics, with either wide or restricted distribution in the BAF, as far as were structured within the biome. Thus, each component proposed by the selected studies corresponded to the subgroups defined here.

When necessary, authors were contacted to obtain the full list of localities and/or geographical coordinates mentioned in their studies. Furthermore, whenever the locality name was the only information available, coordinates were checked in the gazetteers accessible via the DIVA-GIS website (www.diva-gis.org). All coordinates were converted to UTM projection.

Some records were eliminated because they were repeated for the same subgroup, either in the same study or in different studies, or no coordinate matched the information available. Also, subgroups with fewer than two records were removed from the analysis, as just one locality recorded is insufficient to define an individualized track. Mixed localities, where the presence of specimens from different subgroups was detected, were multiplied in our dataset for each subgroup occurring there. The full list of groups, subgroups, localities and corresponding references analysed in the present study is provided in the Supporting Information (Table S1).

As sampling has been higher in the southern BAF, we diminished this asymmetry by eliminating redundant individualized tracks (Echeverría-Londoño & Miranda-Esquivel, 2011).

INDIVIDUALIZED TRACKS

The first step of a panbiogeographical analysis consists of drawing an individualized track for each taxon, representing its minimum probable distribution given the occurrence records input. This was done by using a new algorithm for the calculation of the minimum spanning tree, implemented in Martitracks (Echeverría-Londoño & Miranda-Esquivel, 2011).

If the BAF is divided into two components as previously recognized (e.g. Costa, 2003; Moraes-Barros *et al*., 2006; Carnaval & Moritz, 2008; Lara-Ruiz *et al*., 2008), the majority of taxa are expected to be also divided into two subgroups. The subgroups analysed herein belonged to several taxonomic levels, from species and subspecies to populations and lineages. Consequently, each taxon will be represented by two individualized tracks, one in the north and one in the south of the BAF.

Irrespective of the amount of structure found in the surveyed studies, all works differentiating vertebrate

GENERALIZED TRACKS

Overlapping of the individualized tracks is the second step of panbiogeography, originating generalized tracks, which result from the coincidence among taxa distributions (Croizat, 1952). Generalized tracks can be interpreted as biotic components (Morrone, 2009). Again, if there is only a northern and a southern component within the BAF (e.g. Costa, 2003; Moraes-Barros *et al*., 2006; Carnaval & Moritz, 2008; Lara-Ruiz *et al*., 2008), we would expect to obtain two generalized tracks or at least two groups of generalized tracks, latitudinally organized.

This step was also done in Martitracks and tracks were drawn maintaining parameters as the default, except for minimum congruence, which was increased to 0.95. Raising minimum congruence and keeping the cut value and length parameters low allows us to find only the higher similarities between two subgroup distributions (Echeverría-Londoño & Miranda-Esquivel, 2011).

NODES

The last step in a panbiogeographic analysis is the identification and interpretation of nodes. Nodes were manually drawn where the convergence of two or more generalized tracks was depicted. As the location of the convergence was not a unique common locality but different close localities, our nodes represented complexes of nodes (Heads, 2004). Also, given our aim of describing biotic components, nodes corresponded to the limits of biotic components, so we considered them as convergence zones (Heads, 2004). Convergence of the distribution of taxa from distinct taxonomic levels in the same analysis means we are unable to interpret the temporal estimates of nodes. We therefore reviewed the time estimates published for the diversification events of the taxa analysed.

RESULTS

Brazilian atlantic forest vertebrates' endemism components

The areas of endemism for BAF vertebrates defined thus far are depicted in Fig. 1B. According to Haffer's (1969) refugia hypothesis, bird endemism areas are correlated with the refugia, so we also represented the three BAF refugia proposed by Carnaval *et al.* (Carnaval & Moritz, 2008; Carnaval *et al.*, 2009) in our analysis of endemism areas.

The geographical location of the areas itself and the discussions made so far on this topic (Cracraft, 1985; Marinho-Filho, 1996; Stattersfield *et al.*, 1998; Costa *et al.*, 2000; Carnaval & Moritz, 2008; Carnaval *et al.*, 2009; Passos *et al.*, 2010) allowed us to identify four large-scale BAF endemism components, latitudinally and longitudinally organized (Fig. 1B). We named these components according to the consensus endemism area names given in the literature: Pernambuco endemism component (PEec), Bahia endemism component (BAec), Serra do Mar endemism component (Serra do Mar ec), and São Paulo – Paraná endemism component (SP-PRec) (Fig. 1B).

BAF vertebrate panbiogeographical components

Our bibliographic search resulted in approximately 30 studies mentioning a vertebrate's latitudinal differentiation of distribution, including publications in scientifically indexed and non-indexed journals and PhD theses (Table 1). For the spatial panbiogeographical analysis, 23 of these references were used, concerning 22 taxa divided into 58 subgroups, with 37 being endemic, and resulting in 482 occurrence records (see Table S1).

The Martitracks algorithm traced 58 individual tracks and 28 generalized tracks. We were able to group 22 generalized tracks in five overlapping regions (Fig. 2A–E). The other six generalized tracks could not be associated with any of these regions (Fig. 2F–I).

We were able to draw seven vertebrate panbiogeographical convergence zones, corresponding to the complexes of nodes. The convergence zones were divided into four classes of support: (1) PE and RS convergence zones were less supported, corresponding only to the convergence of two and three generalized tracks, respectively; (2) an SC convergence zone was supported by four generalized tracks; (3) Espírito Santo (ES) and SP convergence zones were supported by the convergence of six generalized tracks; and (4) with much higher support, above ten convergent generalized tracks, the nodes in BA and PR were drawn (Fig. 1C).

Considering both the nodes and location of generalized tracks, we defined six vertebrate panbiogeographical components latitudinally and longitudinally organized (Fig. 1C).

As mentioned in the Methods, temporal analysis of the nodes would not be informative, because of the broad taxonomic levels used in the same analysis. Nevertheless, according to the literature reviewed and considering our nomenclature, groups appear to have originated mostly during the Miocene and Pliocene. Their diversification within the BAF, corresponding to our subgroup formation, is most frequently dated to the Pliocene and the Pleistocene. Within-subgroup diversification is the most common event during the Pleistocene, although some population expansions were also reported (Table 1 and references therein).

BAF vertebrate components

Based on the areas of endemism and panbiogeographical analyses we divide the BAF into three major latitudinally organized regions: Northerly BAF (from its northern limit to the São Francisco river), Central BAF (between the rivers São Francisco and Doce; Fig. 1D).

The Northerly BAF is a composite of two components. North 1 (N1) was only recovered by the endemism analysis and North 2 (N2) is limited by a highly supported panbiogeographical convergence zone and by the limit of several areas of endemism. This limit corresponds to the river São Francisco and separates the Northerly BAF from the Central region. We also found two components in the Central BAF, Central 1 (C1) and Central 2 (C2), which are divided by a highly
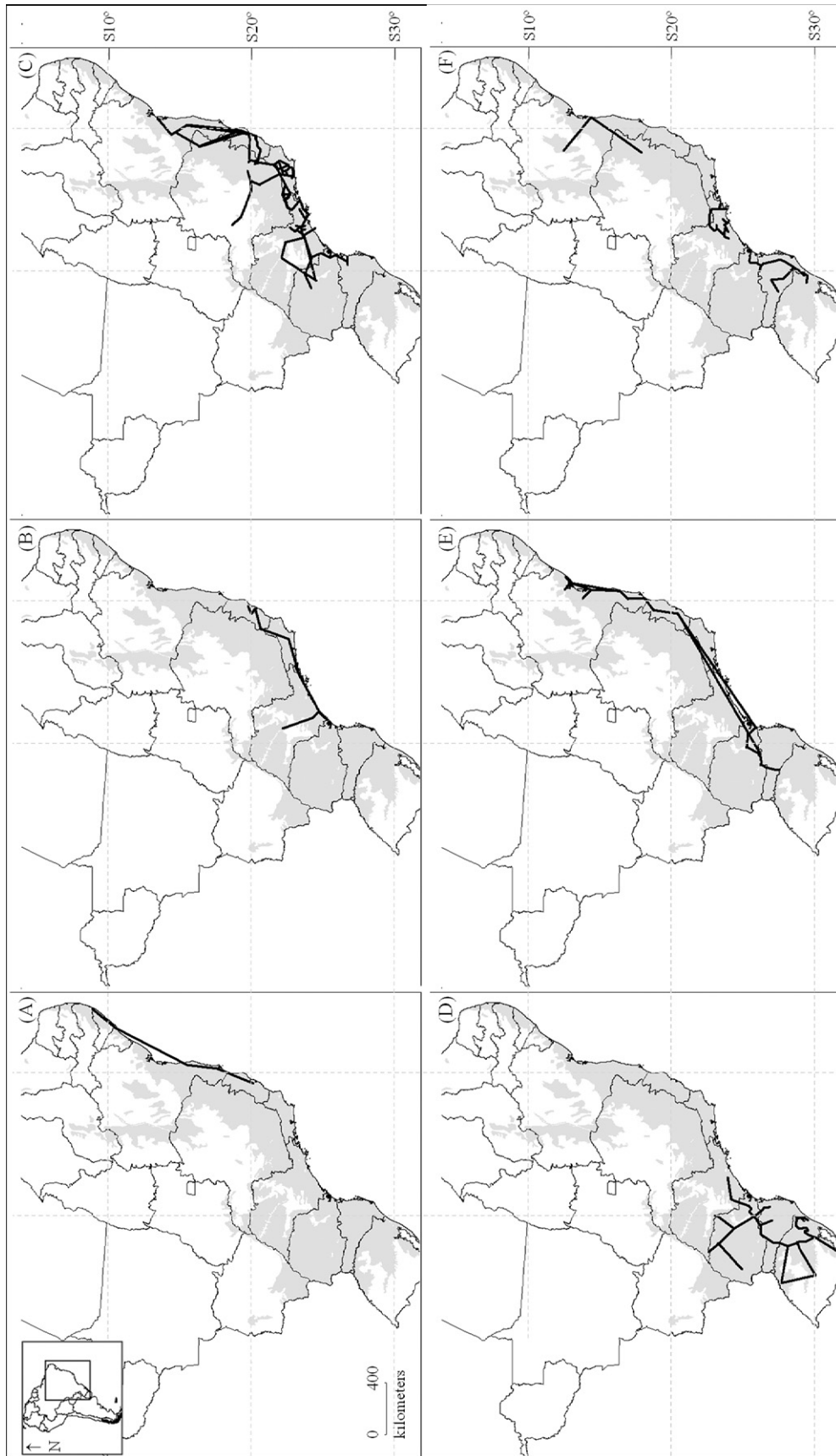
Figure 2. Generalized tracks obtained with a minimum congruence of 0.95. A–E depict groups of two, three, 11, two and four generalized tracks with the same similarity index, respectively. F–I depict tracks that could not be grouped with any other.

supported convergence zone. Similarly, separation from the Southerly BAF is marked by a convergence zone supported by the convergence of six generalized tracks. The Southerly BAF shows longitudinal organization of its vertebrate components (Fig. 1D). Although Southwest 1 (SW1) is corroborated only by areas of endemism, the Southwest 2 (SW2) component is not only corroborated by the Paraná's centre of endemism (Cracraft, 1985) but is also delimited by the convergence zones of PR and SC. Also, the Southeast (SE) component is corroborated by the Serra do Mar endemism areas (and the moderately supported convergence zones ES and SP). South 1 (S1) and South 2 (S2) are divided by the limits of bird endemism areas (Cracraft, 1985; Silva *et al.*, 2004). S2 is supported only by panbiogeography, with the southern convergence zone being found in RS, the BAF's southern limit (Fig. 1B–D).

DISCUSSION

The definition of components based on overlap of described areas of endemism was not as objective as that based on panbiogeography. Fewer studies were available concerning the latter, and considering very distinct geographical regions and scales. We were able to identify only large-scale components of BAF endemism, grouping smaller areas of endemism within the larger ones, and mostly based on arguments and discussions published to date (Cracraft, 1985; Marinho-Filho, 1996; Stattersfield *et al.*, 1998; Costa *et al.*, 2000, 2004; Carnaval & Moritz, 2008; Carnaval *et al.*, 2009; Passos *et al.*, 2010; Fig. 1B).

The southern BAF endemism components were more difficult to delimit, as the overlap of endemism areas was less consensual. However, the evidence for bird endemism areas in the Serra do Mar (Stattersfield *et al.*, 1998; Silva *et al.*, 2004), the distinctiveness of this region compared with areas to the south-west (Cracraft, 1985), and the less pronounced differences found in the south-southwest area (Cracraft, 1985; Marinho-Filho, 1996; Costa *et al.*, 2000; Carnaval & Moritz, 2008; Carnaval *et al.*, 2009; Passos *et al.*, 2010) prompted us to divide these regions into two components (Fig. 1B). By contrast, the PEec is well supported by several areas of endemism (Stattersfield *et al.*, 1998; Costa *et al.*, 2000; Silva *et al.*, 2004). Between the Serra do Mar ec and PEec we have delimited the BAec, limits of which are corroborated by Silva *et al.* (2004) and Carnaval *et al.* (Carnaval & Moritz, 2008; Carnaval *et al.*, 2009).

The broader scale of endemism area components is also related to the fact that their definition is focused on taxa at the species level, while panbiogeography can find patterns at a finer taxonomic scale (Morrone, 2009). Panbiogeography allows us to analyse not only

Table 1. Description of studies reporting a differentiation in the forest-dependent vertebrate distribution within the Atlantic forest

	Taxonomic group	No. of individuals sampled	No. of localities sampled	Taxonomic subgroups	Time estimates (Myr)	Reference(s)
Reptiles	*Bothrops leucurus**	104 morphology 18 genetics	7	Bahia	No data	Puorto *et al.* (2001)
	*Gymnodactylus darwinii**	42	22	Espírito Santo Northern Doce river Between Doce and Paraguaçu rivers Southern Paraguaçu river	No data	Pellegrino *et al.* (2005)
	*Bothrops jararaca**	171	94	From Espírito Santo to São Paulo From Paraná to Rio Grande do Sul	5.1-6.0 (group formation) 3.8 (subgroups formation) 0.14-0.76 (diversification within subgroups) 0.1 (southern subgroup expansion)	Grazziotin *et al.* (2006)
Birds	*Tangara*	7	4	Alagoas (two species) Pernambuco São Paulo	3.5-5.5 (group formation)	Burns & Naoki (2004)
	*Xiphorhynchus fuscus**	114 (max.)	26 (max)	Alagoas, Serras de Baturité and Ibiapaba Bahia and northern Minas Gerais Southern Minas Gerais and Rio de Janeiro From São Paulo to Rio Grande do Sul	3 (group formation) 0.11–0.79 (subgroups formation) 0.19 (southern subgroup expansion) and 0.57 (centre subgroup expansion)	Cabanne *et al.* (2007, 2008)
	*Thamnophilus ambiguous**	22	10	Central Bahia and north-eastern Minas Gerais Bahia, south-eastern Minas Gerais and Espírito Santo	0.9–3 (group formation)	Lacerda *et al.* (2007)
	*Conopophaga lineata**	77	21	Southern Bahia to Northeastern Minas Gerais South-eastern Minas Gerais to north-eastern São Paulo São Paulo and Paraná Rio Grande do Sul to Misiones Argentina	0.22–1.7 (subgroups formation) 0.04–0.18 (southern subgroups expansions)	Pessoa (2007)
	*Conopophaga melanops**	32	11	Pernambuco and Alagoas Bahia to São Paulo	0.04–0.65 (subgroups formation) 0.02–0.06 (northern group expansion) 0.01–0.09 (southern group expansion)	

Table 1. *Continued*

Taxonomic group	No. of individuals sampled	No. of localities sampled	Taxonomic subgroups	Time estimates (Myr)	Reference(s)
Birds (cont.)					
*Sclerurus scansor**	49	27	Ceará / From Bahia to the north of São Paulo / From southern São Paulo to Rio Grande do Sul	1.12 (group formation) / 0.09–0.60 (subgroups formation)	D'Horta *et al.* (2011)
*Dendrocolaptes platyrostris**	25	12	Minas Gerais to São Paulo / Paraná to Rio Grande do Sul	0.05 (diversification within subgroups) / < 0.05 (southern subgroup expansion)	Cabanne *et al.* (2011)
Thoropa miliaris complex*	137	43	Espírito Santo / Espírito Santo, Minas Gerais and Rio de Janeiro / São Paulo / Juréia (São Paulo)	9–12 (group formation) / 8.1–3.1 (subgroups formation) / 0.2–4.7 (diversification within subgroups) / 0.15–0.16 (southern subgroups expansion), 0.14–0.45 (northern subgroups retraction), and 0.15–0.2 (northern subgroups expansion)	Fitzpatrick *et al.* (2009)
*Eleoscytalopus indigoticus**	11	6	Bahia, Minas Gerais and Rio de Janeiro / Paraná	6.2 (groups formation) / 2.4 (subgroups formation) / 0.6 (diversification within subgroups)	Mata *et al.* (2009)
*Scytalopus**	21	22	Bahia / Minas Gerais / São Paulo and Paraná / Paraná and Santa Catarina / Rio Grande do Sul	9.0 (groups formation) / 0.6 (diversification within subgroups)	
Mammals					
*Trinomys**	69 (max.)	23 (max.)	Sergipe / Western slope of the mountains, Bahia and Rio de Janeiro / From Serras do Mar and da Mantiqueira to the coast	10 (group formation) / 1.6–7.7 (subgroups formation)	Lara & Patton (2000); Galewski *et al.* (2004)
*Bradypus variegatus**	47 (max.)	4 geographical regions	Alagoas (and Maranhão) / Bahia and Minas Gerais / São Paulo	No data	Moraes-Barros, Morgante & Miyaki (2002); Moraes-Barros *et al.* (2006, 2007)
Rhipidomys and *Micoureus*	Without data	13	Bahia, Espírito Santo and North of Minas Gerais / South of Minas Gerais, Rio de Janeiro and São Paulo	No data	Costa (2003)

Table 1. *Continued*

Taxonomic group		No. of individuals sampled	No. of localities sampled	Taxonomic subgroups	Time estimates (Myr)	Reference(s)
Mammals (cont.)	*Metachirus nudicaudatus*	Without data	6	Bahia	No data	Costa (2003)
	*Bradypus torquatus**	70 (max.)	9 (max.)	From Espírito Santo to São Paulo Bahia Espírito Santo and Rio de Janeiro	1.44–2.48 (subgroups formation) 0.13–0.32 (diversification within subgroups)	Moraes-Barros *et al.* (2006); Lara-Ruiz *et al.* (2008)
	*Euryoryzomys russatus**	13	8	Minas Gerais and Rio de Janeiro From São Paulo to Rio Grande do Sul	No data	Miranda *et al.* (2007)
	*Akodon cursor**	50	11	Pernambuco and Bahia From Espírito Santo to São Paulo Cardoso's Island	No data	Nogueira & Fagundes (2008)
	Lonchorhina aurita	12	4	Pernambuco Espírito Santo São Paulo	No data	Lopes & Ditchfield (2009)
	*Micoureus**	23 (max.)	7	Bahia Minas Gerais and Rio de Janeiro	No data	Dias *et al.* (2010)
Amphibians	*Hyla**	Without data	28	Bahia and Minas Gerais From Espírito Santo to Paraíba do Sul river valley From Paraíba do Sul river valley to São Paulo	No data	Napoli (2000, 2005)
	*Hypsiboas bischoffi**	269	34	São Paulo and northern Paraná Southern Paraná to Rio Grande do Sul	No data	Marcelino *et al.* (2009)
	*Phyllomedusa burmeisteri complex**	72	30	From Sergipe to MinasGerais From Espírito Santo to São Paulo From São Paulo to Santa Catarina (eastern subgroup) From São Paulo to Santa Catarina (western subgroup)	5 (group formation) 1.6–2.5 (subgroups formation) 0.4 (diversification within subgroups)	Brunes *et al.* (2010)
	*Rhinella crucifer group**	65 (max.)	40	Paraíba, Pernambuco and Bahia/ Minas Gerais and Espírito Santo Espírito Santo to Paraná/Santa Catarina Rio Grande do Sul	6.26 (group formation) 0.84–3.97 (subgroups formation) 0.24–0.31 (diversification within subgroups)	Thomé *et al.* (2010)

*Taxa used in the panbiogeographical analysis.

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endemism at a species' taxonomic level, but several taxonomic levels, either endemic or not. The two approaches are not expected to give coincident results, and instead they were compared because of their complementarity (Morrone, 2009). Thus, the four vertebrate components defined by the previously described areas of endemism, added to the six panbiogeographic vertebrate components identified here, allowed us to delimit nine vertebrates components grouped into three main regions (Fig. 1B–D).

This division is far from resembling the simple division into two components proposed earlier (e.g. Costa, 2003; Moraes-Barros et al., 2006; Carnaval & Moritz, 2008; Lara-Ruiz et al., 2008). Furthermore, the vertebrate components identified herein are not only distributed latitudinally but also highlight an east–west differentiation.

In our panbiogeographic approach we had to use different taxonomic levels. Per se this already is indicative of complexity, suggesting that concurrent events in time were not responsible for the taxa diversification within the BAF. Consequently, we were not able to match the empirical time estimates reviewed with the formation of the components identified here. Yet our review highlights that vertebrate diversification events are older than previously thought. Refugia theory (Haffer, 1969) and Pleistocene climate changes are often cited as plausible explanations for the origin of vertebrate species or population structure in the BAF (e.g. Carnaval & Moritz, 2008; Thomé et al., 2010). However, several diversification events are dated to as early as the Miocene (Galewski et al., 2004; Grazziotin et al., 2006; Fitzpatrick et al., 2009; Thomé et al., 2010; Table 1). This does not exclude a Pleistocene influence. Two well-sampled forest-dependent vertebrate groups diversified, expanded and lost genetic diversity probably in response to Pleistocene changes (D'Horta et al., 2011; G. S. Cabanne & C. Y. Miyaki, unpubl. data).

The multitude of diversification events across both time and space, and the different population responses inferred from the studies cited here, leads us to agree with previous statements for the Amazonian forest (Bush, 1994). It is not likely that a simple event in such a small period of time (the Pleistocene epoch) would provide all the biodiversity found in the BAF.

The present work allows us to go beyond the assumption of complexity of the BAF, and to propose a hypothesis for the organization of its diversity. The biome's complexity is now reflected in the high number of vertebrate components herein described. We consider that is necessary to understand the diversifying processes that have affected the BAF by using small-scale studies before evaluating the larger

events that influenced the biome as a whole. Our proposal is to divide the BAF focusing either on the biotic convergence zones or on the biotic components in future historical biogeography analyses. We believe that despite the amount of data already accumulated, it is not yet possible to propose a complete and consistent hypothesis for the origin of the BAF's biodiversity. However, our new approach to analyse the biome as partitioned here may be more fruitful if given the evidence discussed below.

THE NORTHERLY BAF – PATCHINESS AND CLIMATIC INSTABILITY

According to the areas of endemism, this region should be considered a unique component. Also, the convergence zone which divides the two components is supported only by the convergence of two generalized tracks, which meet from the south (Fig. 2A). Sampling available for the panbiogeographical analysis was limited in N1, with no coincident distributions, above the convergence zone (Fig. 2, supporting Table S1). In fact, the literature available largely relate to new species descriptions (Alves et al., 2006, 2009; Lingnau, Canedo & Pombal Jr., 2008), with some species being reported only from their type localities (Canedo, Dixo & Pombal, 2004; Carnaval & Peixoto, 2004; Cruz & Pimenta, 2004). In this context we believe that further studies are necessary to describe more accurate species distributions within this region, allowing better use of the panbiogeographical tools.

Nevertheless, we chose to describe two vertebrate components within the Northerly BAF, not only because of the panbiogeographical convergence zone, but also because this regions is shown to be one of the most important connection bridges between the Atlantic and the Amazonian forests for mammals (Costa, 2003; Moraes-Barros, Miyaki & Morgante, 2007; Tchaicka et al., 2007) and for birds (Ribas & Miyaki, 2004; Cabanne et al., 2008; Vilaça & Santos, 2010) and for the colonization of the eastern Atlantic coast by amphibians (Carnaval & Bates, 2007). Also, there is evidence that the northern Atlantic coast was the most probable route linking those forests (De Oliveira, Barreto & Suguio, 1999; Silva & Bates, 2002). So, a component influenced more by the connection with Amazonian forest, corresponding to N1, and another related more to the Atlantic forest itself, N2, seems to be more plausible. All taxa used in the present analyses are forest-dependent, so a connection must have been made through forest expansion. Nevertheless, some authors point to a forest spreading only in the Quaternary (Auler et al., 2004a, b), and others suggested that periods of major humidity favouring forest expansion could have been of short

duration (Wang *et al.*, 2004). Either way this territory seems to have been marked by a complex heterogeneous climate, with abrupt changes between wet and dry phases (Auler *et al.*, 2004a; Wang *et al.*, 2004). The Northerly BAF is even today marked by a climate that is strongly influenced by monsoons, being hot and arid in some areas and fully humid in others (Kottek *et al.*, 2006). These climatic asymmetries resulted in a patchy landscape in which Atlantic montane forest enclaves, called *brejos de altitude*, occur surrounded by drier areas, mostly within the Caatinga biome. These enclaves are still present, even with the severe dry periods of this region (Hastenrath, Wu & Chu, 1984).

Climatic instability and heterogeneity were probably responsible for speciation by local adaptation or allopatry, as climatic difference may have enhanced population isolation in less perturbed or less susceptible, smaller regions (Zamudio & Green, 1997; Hewitt, 2000; Cabanne *et al.*, 2008). Also, amphibian species appear to be highly structured (Carnaval, 2002) and the different communities seem to have been affected by past local events, climatic and landscape changes, experiencing different responses to these changes, either recolonization, extinction or population expansion. A diversifying process similar to the refuge theory (Haffer, 1969) would be a reasonable null hypothesis to be tested in this region.

This has been done considering the BAF as a whole, but given our results, a small-scale evaluation should be more valuable to disentangle the biogeographical history within the Northerly BAF. As we will demonstrate, other processes of diversification, distinct from the refugia hypothesis, may have been more important in the other BAF regions.

THE CENTRAL BAF – STABILITY AND THE ROLE OF THE DOCE RIVER

In contrast to the two vertebrate components described for the Northerly BAF, the two Central vertebrate components are highly equally supported by the endemism areas analysis and panbiogeography. The convergence zone which divides the two components corresponds to the convergence of more than ten generalized tracks and the delimitation of this region is made by two biogeographically important rivers, the São Francisco and Doce. Both had been mentioned as limits of areas of endemism (Cracraft, 1985; Costa *et al.*, 2000; Carnaval & Moritz, 2008; Carnaval *et al.*, 2009), and as potential barriers or taxa distribution limits (Pellegrino *et al.*, 2005; Cabanne *et al.*, 2008; Carnaval & Moritz, 2008; Lara-Ruiz *et al.*, 2008; Thomé *et al.*, 2010).

The Central BAF has a clear vertebrate differentiation (Miranda *et al.*, 2007; Lara-Ruiz *et al.*, 2008) and hold greater genetic diversity (Marinho-Filho, 1996; Moraes-Barros *et al.*, 2006; Cabanne *et al.*, 2008, 2011; Fitzpatrick *et al.*, 2009; Thomé *et al.*, 2010; D'Horta *et al.*, 2011) in comparison with the other BAF regions. As a consequence, many studies address this region as a stable area, for reptiles (Grazziotin *et al.*, 2006), birds (Cabanne *et al.*, 2008), amphibians (Carnaval & Moritz, 2008; Fitzpatrick *et al.*, 2009), and mammals (Carnaval *et al.*, 2009).

This stability has been linked to rivers, particularly the Doce (Puorto *et al.*, 2001; Pellegrino *et al.*, 2005; Grazziotin *et al.*, 2006). Based on these three studies, the role of the Doce river as a biotic convergence zone has been inferred (Cabanne *et al.*, 2008; Carnaval & Moritz, 2008; Lara-Ruiz *et al.*, 2008; Thomé *et al.*, 2010). However, no formal test was made to confirm the riverine barrier hypothesis (Ayres & Clutton-Brock, 1995) in the BAF, and no alternative hypotheses were proposed to explain why the Doce river is a barrier to dispersal, whereas other major rivers are not (Pellegrino *et al.*, 2005).

An alternative explanation for the distinct groups north and south of the Doce river may be related to distinct topographies. The north-east area is at lower altitude than the south-east (Oliveira-Filho & Fontes, 2000). Immediately south of the Doce river are the two highest peaks of the BAF mountain ranges (> 2800 m), in the hills of Caparaó (IBGE, 2006). And altitude is significantly correlated with species composition (Machado & Fonseca, 2000), even in the southern Doce river (Lara & Patton, 2000). Also vegetation and interspecies competition are factors influencing species distribution near the Doce river (Vilanova *et al.*, 2005).

Across the low altitudes of the Central BAF river valleys, the lowland forest species could penetrate into the continent, over a larger area of suitable habitat (Oliveira-Filho & Fontes, 2000). Low altitudes could also explain the more extended sea influence, resulting in the absence of marked climatic changes (Anhuf *et al.*, 2006). In contrast to the Northerly BAF, the constancy of the climate must have enhanced diversification of taxa as a result of adaptation to micro-habitats available in this region. The Central BAF's vegetation richness (Martini *et al.*, 2007) also favours this hypothesis, with the wide plant diversity supporting the diversification of all other organisms.

THE SOUTHERLY BAF – HOW RECENTLY WAS IT FORESTED?

The Southerly BAF has the highest number of vertebrate components proposed. On the one hand, areas of

endemism were less concordant than in the other regions (see Discussion above). On the other hand, the number of distribution records available for the panbiogeographical analysis was higher in the southeast part of the region. Therefore, in SW1 less sampling was available for both analyses, prevailing the presence of a Pleistocene refugium in this region (Carnaval & Moritz, 2008; Carnaval *et al.*, 2009), and S2 is only supported by panbiogeography. The fact that several species have their limit of distribution in this region (IUCN, 2010) also contributed to defining the location of the convergence zone, as the panbiogeography mostly relate to taxa distributions (Croizat, 1952). All other components are corroborated by both analyses used.

Of note is the marked east–west differentiation, which was not previously highlighted, but is present in several studies analysed (Cracraft, 1985; Lara & Patton, 2000; Brunes *et al.*, 2010). This longitudinal organization is possibly a result of the more inland extension of the BAF within this region, despite evidence of an east–west differentiation also being present in the Central region, particularly in C2 (Fig. 1D; Lara & Patton, 2000; Silva *et al.*, 2004; Dias *et al.*, 2010).

However, as explained in the previous section, the Central BAF probably evolved under climatic stability, given its low altitude. By contrast the Southerly BAF has the biome's highest mountain ranges (IBGE, 2006). These mountains are responsible for amphibian and bird lineages and species restriction and isolation within this area (Stattersfield *et al.*, 1998; Burns & Naoki, 2004; Grau *et al.*, 2005; Napoli, 2005). The reason behind this isolation remains controversial. Uplift of the Serra do Mar and Mantiqueira mountain systems appears to be correlated with the isolation of forested-dependent mammals, differentiating the east from the west (Galewski *et al.*, 2004; re-analyses of Lara, Geise & Schneider, 2005). Conversely, evidence for recent population expansions corroborate a more recent onset of forest within the Southerly BAF (Grazziotin *et al.*, 2006; Martins *et al.*, 2007, 2009; Miranda *et al.*, 2007; Cabanne *et al.*, 2008, 2011; Fitzpatrick *et al.*, 2009; D'Horta *et al.*, 2011). Furthermore, support for this hypothesis is provided by the fact that the local topography seems to have suffered marked modification across time, as many river piracy events are evident (Oliveira & Neto, 2007), and the signs of an intense tectonic activity are still apparent (reviewed by Saadi, 1993 and Ribeiro, 2006). These early topographic changes, the altitude itself and the past cold fronts from Antarctic in the late Quaternary made the Southerly BAF unsuitable for an exuberant forest on several occasions (reviewed by Behling, 2002), resulting in the current very distinct floristic pattern

(Oliveira-Filho & Fontes, 2000). Thus, geographical vicariance and ecological vicariance could have led to the vertebrate differentiation reported.

Moreover, the role of connectivity established by gallery forests remains unresolved. It seems to have promoted the dispersal of taxa between the Atlantic and the western Amazonian forests (Costa, 2003; Fernandes *et al.*, 2004), or expansion of taxa within Cerrado and vice versa (Silva, 1996). A southern route of faunal exchange between the Atlantic and the Amazonia forests through the Pantanal is also supported (Costa, 2003; Martins *et al.*, 2009).

Our review supports that shifts between isolation and connectivity characterize the distinct history of the Southerly BAF (Costa *et al.*, 2000; Carnaval & Moritz, 2008; Carnaval *et al.*, 2009). But the time when these events occurred, and their influence on the distribution and extension of forest remains controversial.

CONCLUSIONS

This paper summarizes current knowledge on vertebrate diversity patterns within the BAF and help our understanding of its biogeographical history. Besides showing a latitudinal differentiation, the BAF has a considerably more complex and intricate structure than the northern and southern components previously suggested. We describe nine components grouped within three main regions, latitudinally and longitudinally organized, and transverse to several vertebrate taxa. We also show that this pattern was created throughout the Pleistocene, but earlier events, as early as the Miocene, also influenced the distribution and diversification of taxa. The previously proposed northern and southern divergence is probably due to poor sampling or in some cases is just an outcome pattern observed in species whose distribution is restricted to part of the BAF. We believe that analysing separately the BAF vertebrate components and convergence zones proposed herein will contribute more effectively to understanding the biome's biogeographical history.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Data analysed in the panbiogeographical approach.

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