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Perspective

Biogeographic patterns, origin and speciation of the endemic birds from eastern Brazilian mountaintops: a review

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We review the main biogeographic and phylogenetic hypotheses about the origin and distribution of the endemic birds from Brazilian mountaintops, a heterogeneous group composed of hummingbirds and passerines living in high-altitude open habitats of *campos rupestres*, *campos de altitude* and *campos sulinos* from southern to north-eastern Brazilian mountaintops (Espinhaço Range, Serra do Mar, Serra da Mantiqueira and Serra Geral). Some authors consider that these birds are probably closely related to other species distributed in cooler areas of South America. We used ranges of these birds, spatial pattern and discontinuities in the distribution of phytophysiognomies to determine potential geographic barriers to dispersal and centres of origin and speciation. We reanalysed biogeographical hypotheses regarding the evolution of the endemic birds from Brazilian mountaintops and their habitats in the light of recent phylogenetic reconstructions that included some of these species. The evolutionary histories of the species *Augastes scutatus*, *Augastes lumachella*, *Formicivora grantsaui*, *Polystictus superciliaris* and *Embernagra longicauda* are difficult to assess due to lack of phylogenies that establish their systematic position. For *Asthenes luizae*, *Asthenes moreirae*, *Cincludes pabsti* and *C. espinhacensis*, the phylogenies estimate also their lineage divergence times, which allows for inferences concerning connections between the biota of eastern Brazil, southern South America and the Andean mountains. We also identified 26 lowland regions between the mountains that were potentially barriers to dispersal. Phylogenetic relationships strongly highlight the importance of connecting paths and speciation through the south, especially in the cooler areas in South America. These patterns show that eastern Brazil, southern South America and the central and northern Andes are four important centres of origin and radiation for the endemic birds from the eastern Brazilian mountains.

Key words: *campos de altitude*, *campos rupestres*, disjunct distribution, Espinhaço Range, geographic barriers, highlands, phylogeny, relictuation, Serra da Mantiqueira, vicariance

Introduction

The mountains of eastern Brazil harbour a rich diversity of soils and rocky substrates, a variety of micro-climatic regions and a complex vegetation cline along altitudinal gradients that supports a high rate of plant endemism (Giullietti, Pirani & Harley, 1997; Harley, 1995; Rapini, Ribeiro, Lambert, & Pirani, 2008; Safford, 1999). Relatively little is known about the ecology, biogeography and natural history of this endemic montane biota (Behling, 1998; Rapini,

Ribeiro, Lambert & Pirani, 2008). Endemic birds of the mountaintops in eastern Brazil form a heterogeneous group of species of hummingbirds and passerines living in unique high-altitude habitats known as High Altitude Rocky Complexes (Benites, Shaefer, Simas, & Santos, 2007; Freitas, Chaves, Costa, Santos, & Rodrigues, 2012; Vasconcelos, 2008). These habitats are characterized by a series of open vegetation types and are restricted to the highest areas of the mountains and hills from south-eastern to north-eastern Brazil (Martinelli, 2007; Safford, 1999). The mountain ranges included in this study are the Espinhaço Range (in which the dominant vegetation is *campos rupestres*, usually

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distributed above 900 m); Serra do Mar and Serra da Mantiqueira (both with *campos de altitude* as the dominant vegetation, distributed mainly above 1500 m); and Serra Geral (in which the dominant vegetation is *campos sulinos*) (Fig. 1). These areas are patchily distributed and naturally fragmented, similar to islands of different sizes and distances between them.

Despite these environments having the highest diversity of endemic plants in Brazil (Giullieti, Pirani & Harley, 1997; Martinelli, 2007; Safford, 1999), only 3% of the local avifauna comprise species restricted to the high-altitude open habitats (Vasconcelos & Rodrigues, 2010). Endemic birds from the eastern Brazilian mountains include: two hummingbirds, *Augastes lumachella*, which is restricted to the northern Espinhaço Range (Fig. 2a) and *Augastes scutatus*, endemic to the central-southern Espinhaço Range (Fig. 2b); one antbird, *Formicivora grantsauai*, a recently described species restricted to the northern Espinhaço Range (Fig. 2g); four ovenbirds, *Cinclodes pabsti* is endemic to the Serra Geral in southern Brazil (Fig. 2d), and *C. espinhacensis* was recently discovered at the high elevation *campos rupestres* in the southern Espinhaço Range in the Serra do Cipó region (Fig. 2c), *Asthenes luizae* is restricted to the central-southern Espinhaço Range (Fig. 2e) and *Asthenes moreirae* from the *campos de altitude* of Serra da Mantiqueira and Serra do Mar, and *campos rupestres* of Serra do Caraça in southern Espinhaço Range (Fig. 2f); one tyrant-flycatcher, *Polystictus superciliaris*, which presents populations spread throughout the Espinhaço Range, Serra do Mar, Serra da Mantiqueira and Serra da Canastra (Fig. 2h); and one tanager, *Embernagra longicauda*, widespread throughout the Brazilian mountains (except southern Brazil) with populations on the Espinhaço Range, Serra da Mantiqueira and Serra do Caparaó (Fig. 2i).

Initial systematic studies attempted to classify these species based on their morphological characteristics, ecology, habitat type and behaviour; several authors classified some of these endemic birds with species distributed in the cooler areas of South America, such as southern Brazil, Pampas, Patagonia, Chaco and the high Andes (Fjeldsá & Krabbe, 1990; Schuchmann, 1999; Sibley & Monroe, 1990; Sick, 1985; Silva, 1995). Thus, the isolated occurrence of these species at high altitudes in eastern Brazilian mountains suggests a discontinuity in the distribution of these lineages. Disjunct distributions of populations are a first step in the process of allopatric speciation, a well-recognized part of the evolution of most taxa of Neotropical birds (Aleixo, 2004; Cheviron, Capparella, & Vuilleumier, 2005; Fjeldsá, 1994).

Evidence for inferences regarding the timing of speciation events of endemic birds from Brazilian mountaintops is still scarce, and independent molecular dating approaches could provide important information for the testing and formulation of hypotheses and interpretations

such as those presented here. Recent studies have been conducted to estimate divergence times from cladograms based on DNA mutation rates (Barker, Burns, Klicka, Lanyon, & Lovette, 2013; Burns *et al.*, 2014; Derryberry, Claramunt, Derryberry, Chesser, Cracraft, Aleixo & Brumfield, 2010, 2011; Freitas *et al.*, 2012; Ohlson, Fjeldsá & Ericson, 2008). Even though these figures can be biased, those estimates provide realistic parameters for estimating the time of evolutionary changes.

In this paper, we review the main biogeographic and phylogenetic hypotheses that explain the origin and distribution of the endemic birds from the eastern Brazilian mountains. In the section ‘Biogeographic relationships and landscape evolution’ we discuss the early biogeographic hypotheses about these birds in the context of the geological and climatic changes in South America for each period related to these assumptions. Besides we also discuss how vicariance, dispersion or relictuation processes could have promoted the evolution of these birds. In the section ‘Diversification of the endemic birds from the eastern Brazilian mountains’ we use the recently phylogenetic reconstructions and dating estimates of ancestral lineage splits to reanalyse biogeographic hypotheses and to identify possible centres of origin and speciation in South America. Because there are only a few endemic species in such environments, we detail the analysis of each case in order to discuss and enhance the understanding of events involved in their diversification. In the section ‘Discontinuities and biogeographic barriers in eastern Brazil’ we present the spatial configuration and distribution in ‘islands’ of the high-altitude open habitats and general patterns of the distribution of these endemic birds to determine possible barriers to dispersal. Our approach includes a complete literature review and a detailed examination of issues of systematics, ornithology and biogeography that address the target species of this study, or other taxa treated as related to these birds.

Biogeographic relationships and landscape evolution

The biogeographic history of the South American biota has been explained by many hypotheses, drawing upon different processes related to the history of colonization of the current biogeographic provinces. These include the theory of Pleistocene refugia (Haffer, 1974), the diagonal connections of dry open formations (Vanzolini, 1963) and the seasonally dry tropical forests (Prado, 2000; Werneck, Costa, Colli, Prado, & Sites, 2011). Only a few studies concern the connections between the biota of the eastern Brazilian mountains with other biogeographic provinces of South America (Harley, 1995; Safford, 2007; Sick, 1985; Silveira & Cure, 1993; Simpson-Vuilleumier, 1971; Vielliard, 1990a), and a reappraisal of the biogeographic

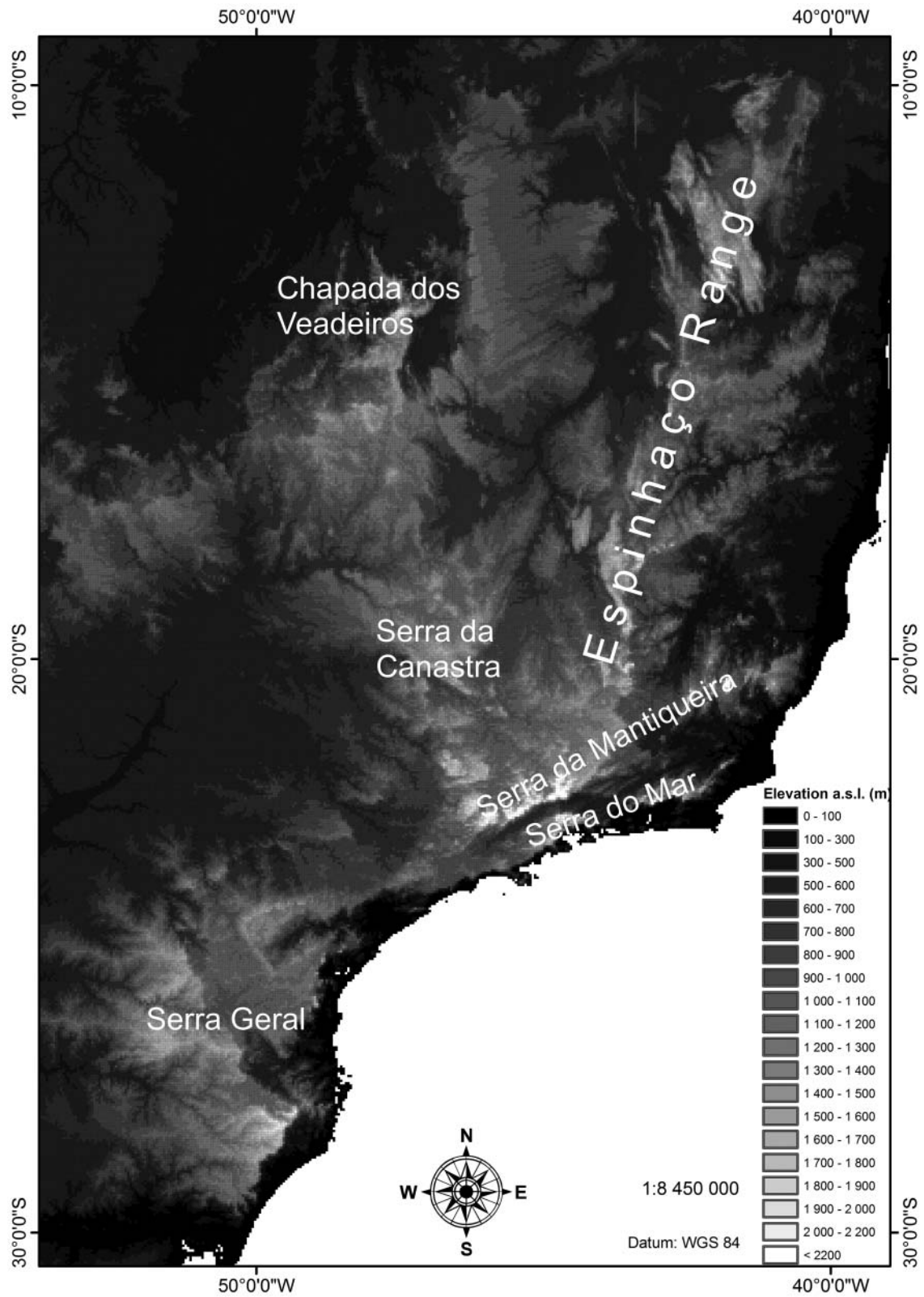


Fig. 1. The main mountain range of Brazil.

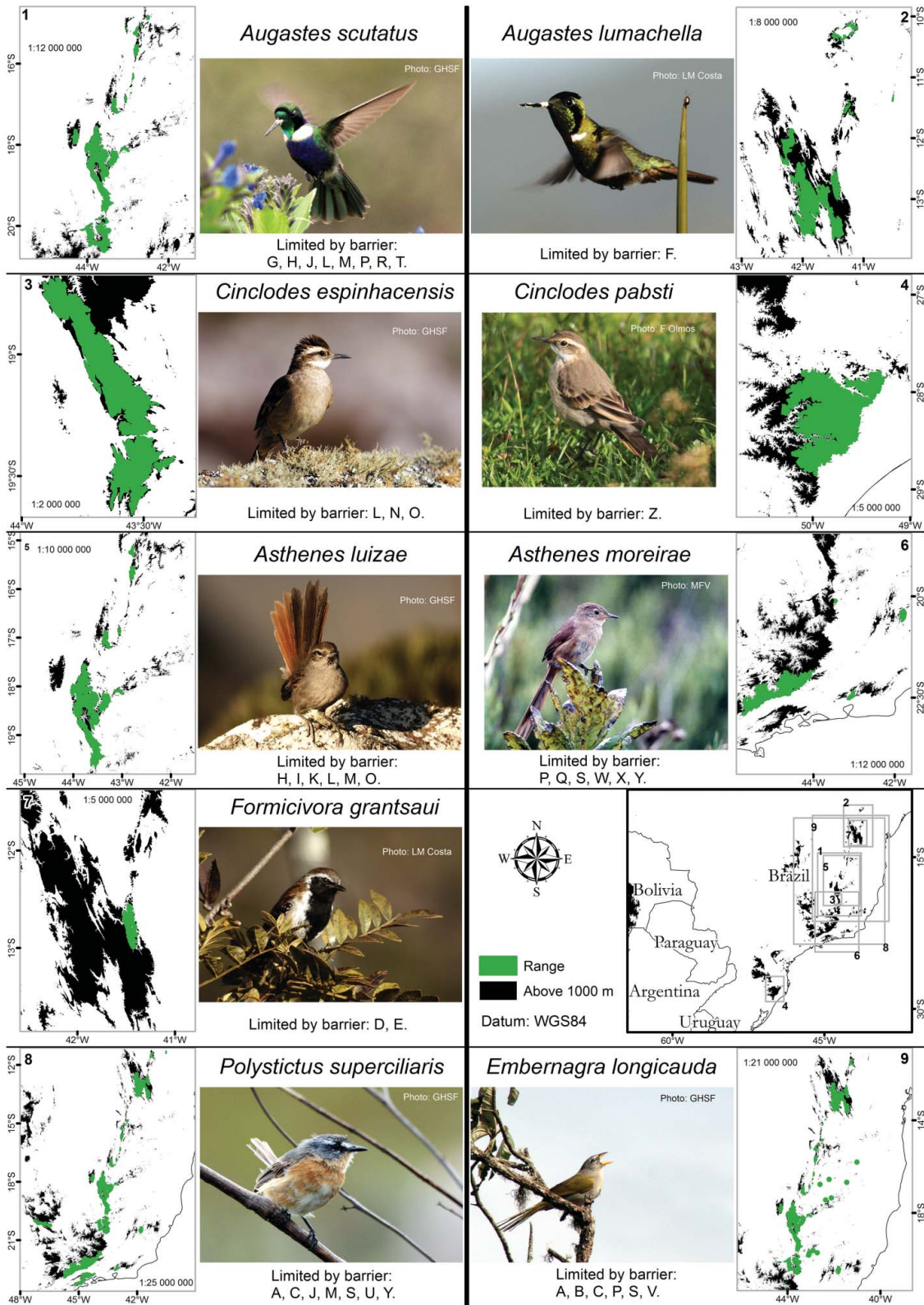


Fig. 2. Geographic distribution of the endemic birds from Brazilian mountaintops. Letters are the geographic barriers shown in Fig. 4.

hypotheses of the endemic birds of eastern Brazilian mountaintops suggests complex sets of distinct evolutionary histories.

Main climate and geological events

It has been assumed that the intensive phase of the Andean uplift in the Middle Miocene was the major geological event that changed the relationships of the biota of most regions in South America. The effect of this tectonic event was the elevation of the Brazilian Plateau and subsidence of the Llanos, Chaco and Pantanal in the Upper Pliocene, and the elevation of Serra do Mar and Serra da Mantiqueira in the Pleistocene (Petri & Fúlvaro, 1983; Silva, 1995; Ortíz-Jaureguizar & Cladera, 2006; Zanella, 2011). The subsidence of Chaco led to extensive marine flooding, aeolian sediment deposition and dry and cold climates culminating in the establishment of xeric vegetation (Iriondo & Garcia, 1993). This geological event split up the South America biota, separating the endemic Brazilian mountaintop birds from their Andean, Pampean, Patagonian and Chacoan relatives. Furthermore, faunal interchange within southern South America was also influenced by various glaciations and successive marine transgressions in the Upper and Middle Miocene that separated the Brazilian Shield from the Andean region and the Guyana Shield (Zanella, 2011). This separation likely occurred in the Late Miocene-Pliocene, forming an arid corridor in Patagonia, and causing the colonization of the southeastern Brazilian highlands and the Andean region (Rabassa, Coronato, & Salemme, 2005).

Biogeographic affinities along similar climatic zones

Remarkable biogeographic affinities have been recognized along the 'V'-shaped cooler areas, from southern Patagonia towards the Andean region and the eastern Brazilian mountains (Sick, 1970, 1985, 1997; Silva, 1995, 1997; Vielliard, 1990a, b; Willis, 1992). In this respect, South American mountains, including the Andes and eastern Brazilian mountains, are proposed to share several taxa with biogeographic affinities along similar climatic zones (Brown, 1987; Fjeldså, Bowie, & Rahbek, 2012; Simpson, 1979; Simpson-Vuilleumier, 1971). Indeed, many congeneric species share disjunct ranges between the southern and south-eastern Brazilian highlands, and between the Patagonian, Pampas, Chaco and Andes, as demonstrated by several groups of organisms, including plants (Fiaschi & Pirani, 2009; Harley, 1995; Safford, 1999), birds (Sick, 1985; Silva, 1995), frogs (Leite, Juncá & Eterovick, 2008), lizards (Rodrigues, 2008; Uzzel, 1959), mammals (Gonçalves, Myers, Vilela, & Oliveira, 2007) and bees (Silveira & Cure, 1993).

Several climate and geological changes created opportunities or adaptive restrictions leading the ancestors of the endemic birds from Brazilian mountaintops to settle into more stable environments, such as the higher areas of eastern South America that are climatically similar to some Andean high-altitude areas (Safford, 1999; Sick, 1985). Although it is assumed that eastern Brazilian mountains were colonized by Andean-Patagonian lineages in the past (Sick, 1985), this biogeographic influence in the local avifauna appears indistinct (Vasconcelos & Rodrigues, 2010). Nevertheless, other studies covering South American biomes as a whole have found a strong relationship between the Andean avifauna, lowland biomes of the Southern Cone of the continent and eastern Brazil (Fjeldså et al., 2012).

Vicariant hypotheses

Some authors have suggested that the origin of these endemic birds is the result of a vicariant event between southern Brazil and the south of the continent during the Pleistocene, when there was a split of ancestral lineages that were distributed in the south of the continent (Sick, 1985; Silva, 1995, 1997; Silva & Bates, 2002). According to these studies, there is strong evidence based on floristic and faunal similarities suggesting that these open vegetation types (savannas) were connected in the past and that vicariant events, more than long-distance dispersal, were responsible for the main biotic disjunctions (Silva, 1995).

Silva (1995) suggested that for distinctive species such as *A. luizae* (and also *E. longicauda*) whose putative relatives live in other South American regions, a vicariant event based on tectonic movements occurred between the Espinhaço Range and several areas including the Chaco, adjacent sub-Andean zone, and the southern Pampas and Patagonia regions.

For *Augustes* spp. that were considered the sister taxon of *Schistes geoffroyi* (from central-northern Andes), Silva (1995) suggested that two vicariant events occurred: the first between the Espinhaço Range and the Andean region, and a second one between different regions (northern and southern) of the Espinhaço Range. This hypothesis considered *A. scutatus* and *A. lumachella* to be sister taxa, as proposed by Gould (1861). Vasconcelos, Chaves, and Santos (2012) suggested that the possible vicariance between the two *Augustes* species may be related to the climate change that occurred in the Plio-Pleistocene.

Pleistocene climatic-vegetation changes

Plio-Pleistocene changes such as tectonics and climatic-vegetation fluctuations led to several hypotheses that explain the speciation of the endemic species of the Cerrado including endemic birds from the eastern Brazilian mountains and their relatives living elsewhere in South

America (Sick, 1985; Silva, 1995, 1997; Silva & Bates, 2002). Another possible scenario suggested by Silva (1997) consisted of a model based on the Pleistocene climatic-vegetational changes, which first caused an expansion of a southern ancestor that followed cold-dry adapted vegetations during a glacial period and, subsequently, a posterior range fragmentation caused by climatic changes during interglacial periods. Finally, there was a rapid differentiation in small relict populations isolated in the Espinhaço Range.

Relictuation of once-widespread ancestral lineage

In addition to the vicariance between the Andean region and the Brazilian shield that split these bird lineages, another process that may have had greater importance in the speciation of ancestral lineages isolated in eastern Brazil was a late relictual process based on adaptation to local distinct conditions in the Brazilian high-altitude open habitats, as is thought to have happened for other birds in the Andean mountains (Garcia-Moreno & Fjelds , 2000). Small isolated populations that were once widespread lineages may have persisted locally due to climate stability in these areas after a tectonic event or macroclimatic changes. This can be exemplified by the effects of the interaction of topographic spatial configuration of mountainous areas with adjacent thermally inert ocean currents (Fjelds  et al., 2012). Birds centres of endemism (or relictual species) in mountainous environments may be the result of the sum of local ecoclimatic stability and complex relief topography (Fjelds , 1994; Fjelds  et al., 2012). Thus, the origin and distribution of these modern relicts are often related to range shifts, and local or regional extinctions weighted by their adaptive capacities (Agarwal, 2001; Habel & Assman, 2010).

Diversification of the endemic birds from the eastern Brazilian mountains

A small number of papers have included the endemic birds from the eastern Brazilian mountains in phylogenetic reconstructions. Recent phylogenetic studies dating the divergence of genera and species help to develop plausible hypotheses related to the environmental changes on the continent through major geological periods, which may have been the source of divergence and ecological specialization for these birds (e.g. Derryberry et al., 2010, 2011; Freitas et al., 2012; Ohlson et al., 2008). Phylogenetic studies describing relationships between the ovenbirds *A. luizae* and *A. moreirae* (Derryberry et al., 2010), and *C. pabsti* and *C. espinhacensis* (Freitas et al., 2012) emphasize the importance of connecting routes and

speciation in the south through the ‘V’ distribution of the South American cooler areas, even as marine transgressions promoting vicariance of widespread ancestral lineages, and later relictuation.

Asthenes luizae and *A. moreirae*

In Derryberry et al. (2010), the systematic position of *A. luizae* has not been resolved, because it represents a deep branch within a trichotomy formed with the two major *Asthenes* clades which comprises two large radiations from the central to northern Andes. In Derryberry et al. (2011), *A. luizae* was in a position basal to the other two *Asthenes* clades, more diversified, but this position presented a low cladistic support. Furthermore, *A. baeri* and *A. dorbignyi* were the deeper sister group of the genus distributed in the Chaco lowlands and central Andes region. Derryberry et al. (2010) showed that *Asthenes moreirae* was closely related to *A. pyrroleuca* (from Patagonian Chacoan region) and *Schizoeaca harterti*. These three species are a sister group of another clade containing other species of the genus *Schizoeaca*, *A. pudibunda* (from western Peruvian Andes) and *A. ottonis* (from southern Peruvian Andes). Phylogenetic reconstructions of Derryberry et al. (2010, 2011) indicate that *A. pyrroleuca* (from Patagonian-Chacoan region) is closely related to *A. moreirae*, but not to *A. luizae*. Indeed, *A. baeri* and *A. dorbignyi* occur in the central and southern Andes and Patagonia, making this explanation more plausible. Following Derryberry et al. (2010, 2011), a more complex relationship can be envisaged between *A. moreirae* and its close relative *A. pyrroleuca*, which is distributed in the extreme south of the continent, and *S. harterti*, which is distributed on the eastern Andean slopes of southern Peru to western Bolivia. Another possible interpretation for the split of ancestral lineages of *Asthenes* between the east and west of the continent is the dispersion from the Andes to southeastern Brazil of ancestral lineages of *A. luizae* and *A. moreirae* at two different times. Indeed, it seems a common pattern for the entire clade Synallaxini which has an Austral–Andean divergence (Derryberry et al., 2011).

Importantly, Silva (1997, Silva & Bates, 2002) classified *A. luizae* (and also *Augastes scutatus* and *Embernagra longicauda*) as Cerrado ‘neoendemics’ which according to the author are species that have their putative sister-taxa in other South American regions, which should not be older than the Plio-Pleistocene transition, c. 2.58 million years ago (mya). However, Derryberry et al. (2011) estimated that ancestral lineages of *A. luizae* diverged approximately 8 ± 1 mya, a period that coincides with the Miocene marine transgressions, while *A. moreirae* diverged more recently, approximately 3 ± 1 mya, and may have arrived in eastern Brazil by dispersion through the highlands of the Brazilian Plateau.

Cinclodes espinhacensis* and *C. pabsti

A phylogenetic study of the *Cinclodes* genus by Chesser (2004) indicated that *C. pabsti* is a sister species to all other *Cinclodes*. The recently described *Cinclodes espinhacensis* is closely related to *C. pabsti*, and together, both species occupy the deepest branch in a phylogenetic reconstruction for the genus *Cinclodes* as a whole (Freitas et al., 2012). Previously, the origin of *Cinclodes* was hypothesized to have occurred in southern South America with a later colonization of the Andes (Chapman, 1926; Irestedt, Fjeldså, Johansson, & Ericson, 2002; Sick, 1973). Moreover, Chesser (2004) and Sanín et al. (2009) found that one clade of the genus originated in the central Andes and the species of the other clade originated in southern South America. Both studies excluded *C. pabsti* (sister to both clades) from their analyses. Recently, Freitas et al. (2012) showed that the Brazilian *Cinclodes* clade diverged from the Andean *Cinclodes* clade between late Miocene/Pliocene, and *C. espinhacensis* and *C. pabsti* separated approximately 220 000 years ago (Late Pleistocene), revealing another important biogeographic connection between the *campos rupestres* of the Espinhaço Range and the *campos sulinos* of the southern Brazilian Serra Geral. Moreover, the Brazilian *Cinclodes* clade represents a remarkable case of relictuation, because allopathic *Cinclodes* species from eastern Brazil likely originated by extinction of intermediate populations, which should exist between these mountain ranges due to climate changes during the Pleistocene.

The separation of the Brazilian *Cinclodes* clade, similar to the isolation of *Asthenes luizae* in the Espinhaço Range, could also be placed in the Late Miocene (Derryberry et al., 2011; Freitas et al., 2012). *Cinclodes* sister groups are *Upucerthia* and *Geocerthia* (Derryberry et al., 2011; Fjeldså et al., 2007) both composed by Andean species and the proposal of a southern origin is consistent with the current range of other species that occupy the deepest branches in the ovenbird phylogeny (Irestedt et al., 2002). This origin is also reflected in the distribution of the monotypic genera of ovenbirds concentrated in the east and south of the continent (Remsen, 2003). The isolation of the Brazilian *Cinclodes* can be associated with some potential geographic barriers that separated ancestral populations, leading to further diversification of two major lineages: one in the Brazilian Shield and another in the Andes and the Pacific coast. The ancestral populations were potentially distributed in the southern Brazilian Shield and adjacent areas, such as the Patagonia and Pampas, corresponding with the southern origin hypothesis.

Augastes lumachella* and *A. scutatus

Augastes lumachella and *A. scutatus* are considered allo-species (Sick, 1997; Vasconcelos, 2008; Vasconcelos

et al., 2012) and are treated as the sister taxon of *Schistes geoffroyi* by various authors (Schuchmann, 1999; Sibley & Monroe, 1990; Silva, 1995; Willis, 1992). In phylogenetic hypotheses presented by Altshuler, Dudley and McGuire (2004); McGuire, Witt, Altshuler, & Remsen (2007); McGuire, Witt, Remsen, Dudley, & Altshuler (2009) and McGuire et al. (2014), *Schistes geoffroyi* appeared as closely related to the genus *Colibri* and, together, formed a sister group to the genus *Doryfera*, in the mango hummingbird group. McGuire et al. (2009) suggested that *Augastes* could also be part of this cluster, although it was not included in the analyses.

Formicivora grantsau

A phylogenetic analysis of the genus *Formicivora* based on morphological and vocal characters (Gonzaga, 2001) was conducted before the description of *Formicivora grantsau*, which has been treated as likely related to *F. rufa*, judging by similar morphological and vocal characteristics (Gonzaga, Carvalhaes, & Buzzetti, 2007). However, it was not possible to determine its systematic position within the group that encompasses its putative closest relatives, *Formicivora acutirostris*, *F. grisea* and *F. rufa* (Gonzaga et al., 2007; Zimmer & Isler, 2003).

Polystictus superciliaris

Polystictus superciliaris is putatively related to *P. pectoralis*, which is typical of open grasslands and has a disjunct distribution in central-southern and northern South American savannas. These species have never been included together in a well-represented phylogenetic analysis that includes several taxa of Tyrannidae (e.g. Chaves, Clozato, Lacerda, Sari, & Santos, 2008; DuBay & Witt, 2012; Ohlson et al., 2008, 2013; Rheindt, Norman, & Christidis, 2008; Tello, Moyle, Marchese, & Cracraft, 2009). Silva (1995) considered *P. superciliaris* as a Cerrado 'palaeoendemic' which according to the author are species that are well established taxonomically, but still have unresolved phylogenetic relationships within their genus or families or have undergone an older rapid process of speciation. Although the hypotheses for the speciation of *P. superciliaris* and *P. pectoralis* remain unresolved, Ohlson et al. (2008) estimated it diverged approximately between 4 to 7 mya, the period of diversification in the group that includes *P. pectoralis*, *Culicivora* and *Pseudocolopteryx*.

Embernagra longicauda

Some recent studies using molecular data have suggested that *Emberizoides ypiranganus*, *Emberizoides herbicola* and *Embernagra platensis* are closely related

and should belong to the Thraupidae family (Barker *et al.*, 2013; Campagna *et al.*, 2011; Klicka, Burns, & Spellman, 2007). Barker *et al.* (2013) and Burns *et al.* (2014) found that *E. platensis* and *E. herbicola* are closely related to *Coryphaspiza melanotis* forming a well-supported clade, and estimated the divergence between *E. platensis* and *E. herbicola* at approximately 3 to 6 mya. Burns *et al.* (2014) named this clade as Emberizoidinae, a new subfamily of grassland tanagers. Again, our species of interest, *Embernagra longicauda*, was not represented in any phylogenetic analyses, but *E. longicauda* and *E. platensis* are very similar in morphology and behaviour, and both were treated as a superspecies by Sibley & Monroe (1990).

Other birds associated with mountaintops

The biogeographic patterns of some other birds with a strong association but not restricted to *campos rupestres* and *campos de altitude*, such as some *Scytalopus* spp. and *Knipolegus nigerrimus*, can provide insights into the colonization and speciation in Brazilian mountaintops.

Brazilian eastern *Scytalopus* birds are mostly found in mountain areas inhabiting the understorey of humid forests and moist slopes with woody vegetation. The phylogenetic study of Mata *et al.* (2009) found that the eastern *Scytalopus* are separated in three well-defined clades, representing lineage breaks between southern and south-eastern Brazil. The oldest divergence occurred in the Middle Miocene between the lineages: *S. speluncae* clade, distributed in Serra do Mar, Serra da Mantiqueira and adjacent; *S. novacapitalis* clade, composed of *S. novacapitalis* from Central Plateau of Brazil, *S. pachecoi* from southern Brazil, *S. diamantinensis* from Chapada Diamantina, Bahia and *S. petrophilus* from Serra do Espinhaço and Serra da Mantiqueira; *S. iraiensis* clade, with disjunct populations from northernmost Minas Gerais and southern Paraná and Rio Grande do Sul states (Mata *et al.*, 2009). Thus, the *S. novacapitalis* clade comprises species with a more interior continental distribution, living in drier habitats. The period of divergence of this clade coincides with climatic changes beginning about 2.5 Mya and splintered populations due to intense glacial cycles. *Scytalopus diamantinensis* was suggested to be sister of *S. petrophilus* (Whitney, Vasconcelos, Silveira, & Pacheco, 2010), which if confirmed, could represent another example of speciation within eastern mountaintops of eastern Brazil, similar to *A. scutatus* and *A. lumachella* vicariance.

Knipolegus nigerrimus is a widespread species with a range throughout the Brazilian mountain areas discussed above, with one subspecies described to *campos rupestres* of the Chapada Diamantina in Bahia (Lencioni-Neto, 1996). Phylogenetic analyses in Hosner & Moyle (2012)

support three clades within *Knipolegus* which appear to have been split by initial vicariance events, followed by subsequent diversification within macro regions, resulting in geographic clusters of closely related species. One most basal clade is confined to northern South America, another clade is confined to the Southern Cone and southern Andes which is sister group of a clade confined to southeast Brazil, comprising *K. nigerrimus*, *K. lophotes* and *K. franciscanus*. This geographic species clusters pattern contrasts to a common allopatric pattern of speciation for Neotropical birds across broad areas (Hosner & Moyle, 2012), as has also been proposed for some sister species of the endemic birds from eastern Brazilian mountaintops.

Importantly, some hypotheses assume that the endemic species of mountainous areas are derived from lowland relatives through colonization by population expansion from adjacent areas, or by long-distance dispersal, or even differentiation of local populations due to large-scale effects on habitat after mountain uplifts (Brumfield & Edwards, 2007; Cracraft, 1994; Ribas, Moyle, Miyaki, & Cracraft, 2007). Overall, a common vicariance history explained most parsimoniously the shared patterns of endemism (Cracraft, 1994). For the psittacid *Pionus*, Ribas *et al.* (2007) showed vicariance and subsequent diversification between lowland/high montane species. The same pattern occurs for the exclusively montane Andean *Haplospittaca* parrots and their lowland sister genus *Pyrilia* (Quintero, Ribas, & Cracraft, 2012). It may be that the lowland/high montane pattern could be related to the *Embernagra longicauda* and *E. platensis* split. McGuire *et al.* (2014) also implied a role for Andean uplift in establishing montane hummingbirds groups.

Centres of origin and connecting routes

In Fig. 3, we outline the possible centres of origin and speciation of the ancestral lineage of endemic birds from the eastern Brazilian mountains as discussed above. The dotted lines **A** and **C** represent the connections between south-eastern Brazil and the central Andes through the southern route. The dotted line **B** represents a possible connection between eastern Brazil and the highlands of central Brazil (Brazilian Plateau), which could be related to the speciation of *A. moreirae* as it is closely related to *S. harterti* (central-northern Andes) and *A. pyrrholeuca* (Patagonian–Chacoan region). Related to this connection, an ancient connection point for *Scytalopus* spp. through the highlands of the Brazilian Plateau was also proposed (Maurício, 2005; Vielliard, 1990a). The dotted line **D** in the Fig. 3 shows a connection represented by a subspecies of hummingbird (*Colibri delphinae greenewalti* Ruschi,

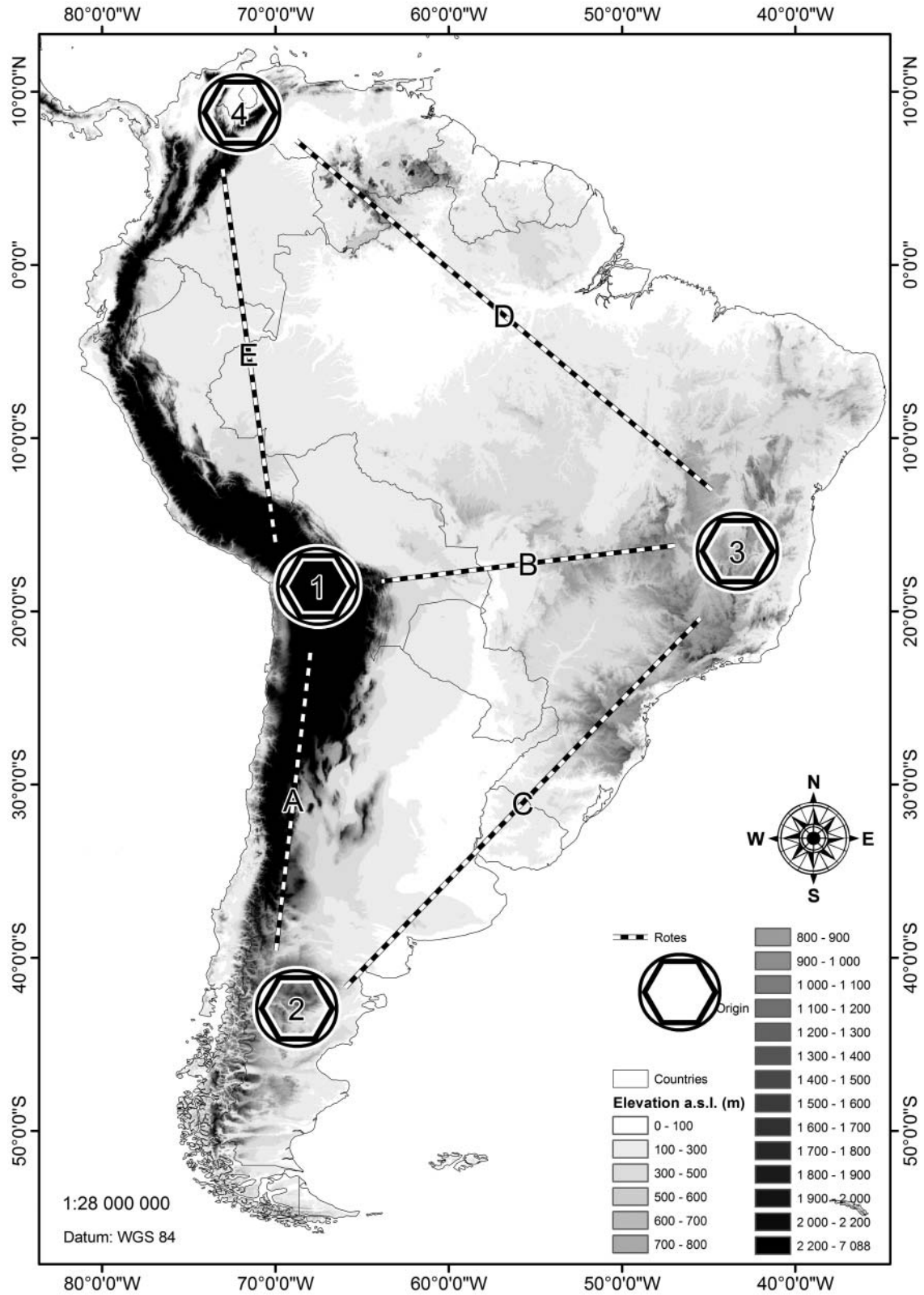


Fig. 3. Biogeographic hypotheses about the origin and occupancy of birds endemic to mountaintops. The numbers represent the possible centres of origin. The letters represent biogeographic relationships between South American cooler areas.

1962), which is recognized as restricted to the *campos rupestres* of the northern Espinhaço Range and is disjunct from its nominal subspecies found in the Guyana Plateau, northern Andes, Central America and island of Trinidad (Schuchmann, 1999). Some plant species also present disjunct distributions in the region of the Guiana Plateau, south-eastern and southern Brazil. Examples of these species include: ferns (Salino & Almeida, 2008); plants of the families Cyperaceae, Eriocaulaceae, Velloziaceae, Xyridaceae (Costa, Trovo, & Sano, 2008; Mello-Silva, 2010; Rapini *et al.*, 2008); the grass *Panicum chnoodes* (Vianna & Filgueiras, 2008); and the bromeliad genera *Dyckia* and *Encholirium*, with centres of diversity located in the Guyanan highlands (Versieux, Wendt, Louzada, & Wanderley, 2008). The dotted line E represents a connection route between possibly related Mango hummingbirds from northern and central Andes with *Augastes* from eastern Brazil.

In some cases, the Brazilian area is suggested as an ancestral homeland of ancient lineages that subsequently colonized the Andean region (Safford, 2007; Sánchez-Baracaldo, 2004; Struwe, Haag, Heiberg, & Grant, 2009). An example of Brazilian origin is the *Chusquea* bamboo, typical of the *Páramos* and patchily distributed in the *campos rupestres* and *campos de altitude* (Safford, 2007). This hypothesis is supported by the relative old age and geological stability of the Brazilian Shield when compared with other South American regions. In particular, the Espinhaço Range is an ancient orographic chain with a Precambrian origin (Saadi, 1995), and it has been much more tectonically stable than the Andes since the Tertiary.

Discontinuities and biogeographic barriers in eastern Brazil

The spatial configuration and distribution in ‘islands’ of the high-elevation open habitats probably played a key role in dispersal, vicariance and relictuation processes, as discussed in the previous sections for each of these endemic species. Occurrence of these vegetation types is strongly conditioned not only by altitude, but also by a combination of landscape variables, such as climatic and topographic conditions, proximity to the ocean and atmospheric circulation (Alvez & Kolbec, 1994; Gontijo, 2008; Vasconcelos, 2011). Thus, determinants for areas of connections or barriers are heterogeneous in every mountainous region. Each island (or archipelago) consists of isolated populations of these endemic birds, and the scale is limited by the size of the mountaintop islands and the connectivity is limited by the distance between them. Discontinuities are caused by lowland areas with distinct habitat types and by the dispersal constraints of each species.

The distribution pattern of each endemic bird from mountaintops can reveal the current barriers that limit their

ranges. In Fig. 4, we present a proposal for identifying these major biogeographic barriers, which are made up of the lowland areas. This division was based on the geographic distributions and recent records for these birds (Vasconcelos, 2008; Vasconcelos, Maldonado-Coelho, & Buzzetti, 2003; Vasconcelos, Lopes, Machado, & Rodrigues, 2008a, 2012; Vasconcelos & Rodrigues, 2010; Chaves, Freitas & Vasconcelos, unpubl data). We considered potential barriers those lowland areas that limit the range of one species, but not of other endemic birds from Brazilian mountaintops. The main areas that represent major barriers for bird species are: between the Serra de São Francisco and central-southern Chapada Diamantina (Fig. 4A; *c.* 100 km, bounding the range of *Polystictus superciliaris* and *Embernagra longicauda*, but not *Augastes lumachella*); between the Chapada Diamantina and central-southern Espinhaço Range (Fig. 4F, G; *c.* 165 km, bounding the range of *Augastes lumachella*, *A. scutatus*, *Asthenes luizae*, *Formicivora grantsau*, but not *Polystictus superciliaris* or *Embernagra longicauda*); between the central-southern Espinhaço Range and Quadrilátero Ferrífero (Fig. 4O; *c.* 16 km, bounding the range of *Cinclodes espinhacensis* and *Asthenes luizae*, but not *Augastes scutatus*, *Polystictus superciliaris* and *Embernagra longicauda*); and the series of lowlands adjoining the Serra da Canastra, Quadrilátero Ferrífero, Serra do Caparaó, Serra dos Órgãos, Serra da Bocaina, Serra da Mantiqueira and Serra Geral.

The complexity of the topology is highly relevant to endemic taxa of *campos rupestres*. Disjunctions have been considered one of the main factors that lead to the high species diversity in these environments (Giulietti *et al.*, 1997). Population genetic studies on plant species from *campos rupestres* have found barriers to gene flow, genetic divergence and geographic structuring among populations of endemic species, as in rupicolous orchids (Borba, Felix, Solferini, & Semir, 2001), *Vellozia gigantea* (Lousada, Borba, & Lovato, 2011), *Vellozia compacta* (Lousada, Lovato, & Borba, 2013), among others. Lousada *et al.* (2013) found geographic structuring between populations from Quadrilátero Ferrífero and the central-southern Espinhaço Range (as proposed in Fig. 4O).

Final considerations

Recent studies have concluded that the series of available museum specimens from eastern Brazil (*campos rupestres*, *campos de altitude* and *campos sulinos*) are not sufficient to study patterns of geographic variation of endemic species (Vasconcelos *et al.*, 2003; Vasconcelos, 2008; Vasconcelos & Pacheco, 2012). Therefore, the high-altitude regions still need sampling because of the lack of data for the taxa discussed above, and new species are still being discovered in remote areas. Good examples of new discoveries are the recent descriptions of

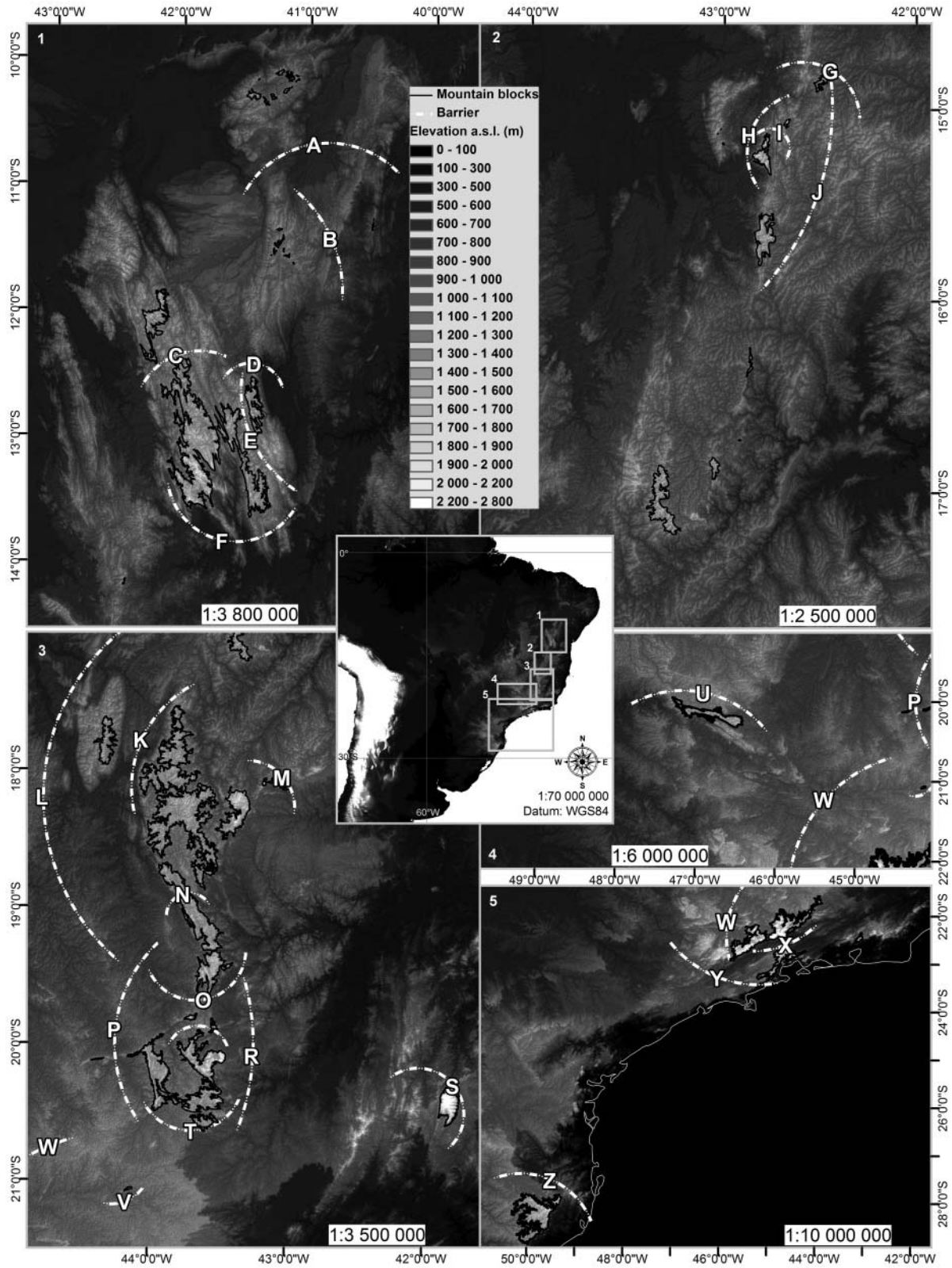


Fig. 4. Geographic barriers (letters) of the mountains complex of Brazil. The main mountain ranges considered in this study are outlined in black (above 1000 m).

Formicivora grantsau (Gonzaga *et al.*, 2007) and *Scytalopus diamantinensis* (Bornschein, Maurício, Belmonte-Lopes, Mata, & Bonatto, 2007) from the Chapada Diamantina in the northern Espinhaço Range, *Scytalopus petrophilus* (Whitney *et al.*, 2010) from the southern area of the Espinhaço Range and Serra da Mantiqueira, and also *Cinclodes espinhacensis* (Freitas *et al.*, 2012). These new species were surprising finds, because both areas of the Espinhaço Range are considered relatively well known in ornithological terms (Melo-Júnior, Vasconcelos, Fernandes, & Marini, 2001; Parrini *et al.*, 1999; Rodrigues *et al.*, 2011; Vasconcelos & Melo-Júnior, 2001).

We noted that the majority of the species have unclear phylogenetic positions, which are mostly based only on external morphological similarities, and as a result, these relationships are not definitive and still require detailed phylogenetic studies. Thus, it is critical to conduct a thorough and systematic treatment of ecology, population dynamics history and collect information about the range, zoogeography and phylogeographic relationships of the birds of the *campos rupestres*, *campos de altitude* and *campos sulinos*, a region in eastern Brazil that is receiving growing international recognition for its high diversity and endemism, designated as part of the Biosphere Reserve, and its increasing biogeographic revelations (Drummond, Martins, Machado, Sebaio, & Antonini, 2005; Freitas *et al.*, 2012; Longhi-Wagner, Welker, & Waechter, 2012; Safford 2007; UNESCO, 2005; and also see Megadiversidade, v.4, Conservation International, 2008).

Finally, throughout this review we show that the time estimates for species diversification suggest that the evolution of the endemic birds of the mountaintops occurred at different times in geological history (the Late Miocene to Pleistocene). It seems that the natural history of these birds cannot be explained by any single or major biogeographic event as previously proposed for the species of Cerrado and *campos rupestres*.

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References

- Agarwal, A.A. (2001). Phenotypic plasticity in the interactions and evolution of species. *Science*, 294, 321–326. doi: 10.1126/science.1060701
- Aleixo, A. (2004). Historical diversification of a terra-firme forest bird superspecies: a phylogeographic perspective on the role of different hypotheses of Amazonian diversification. *Evolution*, 58, 1303–1317. doi: <http://dx.doi.org/10.1554/03-158>
- Altshuler, D.L., Dudley, R., & McGuire, J. A. (2004). Resolution of a paradox: hummingbird flight at high elevation does not come without a cost. *Proceedings of the National Academy of Sciences USA*, 101, 17731–17736. doi: 10.1073/pnas.0405260101
- Alvez, R.J.V. & Kolbek, J. (1994). Plant species endemism in savanna vegetation on table mountains (*Campo rupestre*) in Brazil. *Vegetatio*, 113, 125–139. doi: 10.1007/BF00044230
- Barker, F.K., Burns, K.J., Klicka, J., Lanyon, S.M. & Lovette, I. J. (2013). Going to extremes: contrasting rates of diversification in a recent radiation of New World Passerine birds. *Systematic Biology*, 62, 298–320. doi: 10.1093/sysbio/sys094
- Behling, H. (1998). Late Quaternary vegetational and climatic Changes in Brazil. *Review of Palaeobotany and Palynology*, 99, 143–156. doi: 10.1016/S0034-6667(97)00044-4
- Benites, V.M., Shaefer, C.E., Simas, F.N., B. & Santos, H.G. (2007). Soils associated with rock outcrops in the Brazilian mountain ranges Mantiqueira and Espinhaço. *Revista Brasileira de Botânica*, 30, 569–577. <http://www.scielo.br/pdf/rbb/v30n4/02.pdf>, accessed 19 September 2014.
- Borba, E.L., Felix, J.M., Solferini, V.N. & Semir, J. (2001). Fly-pollinated *Pleurothallis* (Orchidaceae) species have high genetic variability: evidence from isozyme markers. *Annals of Botany*, 88, 419–428. doi: 10.2307/2657106
- Bornschein, M.R., Maurício, G.N., Belmonte-Lopes, R., Mata, H. & Bonatto, S.L. (2007). Diamantina Tapaculo, a new *Scytalopus* endemic to the Chapada Diamantina, northeastern Brazil (Passeriformes: Rhinocryptidae). *Revista Brasileira de Ornitologia*, 15, 151–174. www4.museu-goeldi.br/revistabromito/revista/index.php/.../pdf_464, accessed 19 September 2014.
- Brown, K.S. Jr. (1987). Biogeography and evolution of Neotropical butterflies. In: T.C. Whitmore, & G.T. Prance (Eds.), *Biogeography and Quaternary history in tropical America: Oxford Monographs of Biogeography*, Vol. 3. (pp. 66–104). Oxford: Clarendon Press.
- Brumfield, R.T. & Edwards, S.V. (2007). Evolution into and out of the Andes: A Bayesian analysis of historical diversification in *Thamnophilus* antshrikes. *Evolution*, 61, 346–367. doi: 10.1111/j.1558-5646.2007.00039.x
- Burns, K.J., Shultz, A., Title, P.O., Mason, N.A., Barker, F.K., Klicka, J., Lanyon, M.L. & Lovette, I.J. (2014). Phylogenetics and diversification of tanagers (Passeriformes:Thraupidae), the largest radiation of Neotropical songbirds. *Molecular Phylogenetics and Evolution*, 75, 41–77. doi: 10.1016/j.ympev.2014.02.006
- Campagna, L., Geale, K., Handford, P., Lijtmaer, D.A., Tubaro, P.L. & Loughheed, S.C. (2011). A molecular phylogeny of the Sierra-Finches (*Phrygilus*, Passeriformes): extreme polyphyly in a group of Andean specialists. *Molecular Phylogenetics and Evolution*, 61, 521–533. doi: 10.1016/j.ympev.2011.07.011
- Chapman, F.M. (1926). The distribution of bird-life in Ecuador. *Bulletin American Museum Natural History*, 55, 1–784. <http://digitallibrary.amnh.org/dspace/handle/2246/1244>, accessed 19 September 2014.
- Chaves, A.V., Clozato, C.L., Lacerda, D.R., Sari, E.H.R. & Santos, F.R. (2008). Molecular taxonomy of Brazilian

- tyrant-flycatchers (Passeriformes: Tyrannidae). *Molecular Ecology Resources*, 8, 1169–1177. doi: 10.1111/j.1755-0998.2008.02218.x
- Chesser, R.T. (2004). Systematics, evolution, and biogeography of the South American ovenbird genus *Cinclodes*. *The Auk*, 121, 752–766. doi: 10.1642/0004-8038(2004)121[0752:SEABOT]2.0.CO;2
- Chevron, Z.A., Capparella, A.P. & Vuilleumier, F. (2005). Molecular phylogenetic relationships among the *Geositta* miners (Furnariidae) and biogeographic implications for avian speciation in Fuego-Patagonia. *The Auk*, 122, 158–174. doi: 10.1642/0004-8038(2005)122[0158:MPRATG]2.0.CO;2
- Costa, F.N., Trovo, M. & Sano, P.T. (2008). Eriocaulaceae na Cadeia do Espinhaço: riqueza, endemismo e ameaças [Eriocaulaceae in Espinhaço range: richness, endemism and threats]. *Megadiversidade*, 4, 89–97. <http://www.conservation.org.br/publicacoes/megadiversidade04.php>, accessed 19 September 2014.
- Cracraft, J. (1994). Species diversity, biogeography, and the evolution of biotas. *American Zoologist*, 34, 33–47. doi: 10.1093/icb/34.1.33
- Derryberry, E.P., Claramunt, S., Derryberry, G., Chesser, R.T., Cracraft, J., Aleixo, A... & Brumfield, R.T. (2011). Lineage diversification and morphological evolution in a large-scale continental radiation: the Neotropical ovenbirds and woodcreepers (Aves: Furnariidae). *Evolution*, 65, 2973–2986. doi: 10.1111/j.1558-5646.2011.01374.x
- Derryberry, E.P., Claramunt, S., O'quin, K.E., Aleixo, A., Chesser, R.T., Remsen, J.V.Jr. & Brumfield, R.T. (2010). *Pseudasthenes*, a new genus of ovenbird (Aves: Passeriformes: Furnariidae). *Zootaxa*, 2416, 61–68. <http://www.museum.lsu.edu/brumfield/pubs/pseudasthenes2010.pdf>, accessed 19 September 2014.
- Drummond, G.M., Martins, C.S., Machado, A.B.M., Sebaio, F.A. & Antonini, Y. (2005). *Biodiversidade em Minas Gerais [Biodiversity in Minas Gerais]*. Fundação Biodiversitas, Belo Horizonte.
- Dubay, S.G. & Witt, C.C. (2012). An improved phylogeny of the Andean tit-tyrants (Aves, Tyrannidae): More characters trump sophisticated analyses. *Molecular Phylogenetics and Evolution*, 64, 285–96. doi: 10.1016/j.ympev.2012.04.002
- Fiaschi, P. & Pirani, J.R. (2009). Review of plant biogeographic studies in Brazil. *Journal of Systematics and Evolution*, 47, 477–496. doi: 10.1111/j.1759-6831.2009.00046.x
- Fjeldså, J. & Krabbe, N. (1990). *Birds of the high Andes: a manual to the birds of the temperate zone of the Andes and Patagonia, South America*. University of Copenhagen, Zoological Museum, Copenhagen.
- Fjeldså, J. (1994). Geographical patterns for relict and young species of birds in a Africa and South America and implications for conservation priorities. *Biodiversity and Conservation* 3, 207–226. doi: 10.1007/BF00055939
- Fjeldså, J., Irestedt, M., Jönsson, K.A.I., Ohlson, J. & Ericson, P.G.P. (2007). Phylogeny of the ovenbird genus *Upucerthia*: a case of independent adaptations for terrestrial life. *Zoologica Scripta*, 36, 133–141. doi: 10.1111/j.1463-6409.2006.00270.x
- Fjeldså, J., Bowie, R.C.K. & Rahbek, C. (2012). The Role of Mountain Ranges in the Diversification of Birds. *Annual Review of Ecology, Evolution and Systematics*, 43, 249–265. doi: 10.1146/annurev-ecolsys-102710-145113
- Freitas, G.H.S., Chaves, A.V., Costa, L.M., Santos, F.R. & Rodrigues, M. (2012). A new species of *Cinclodes* from the Espinhaço Range, southeastern Brazil: insights into the biogeographical history of the South American highlands. *Ibis*, 154, 738–755. doi: 10.1111/j.1474-919X.2012.01268.x
- García-Moreno, J. & Fjeldså, J. (2000). Chronology and mode of speciation in the Andean avifauna. *Bonn Zoological Monographs*, 46, 25–46. xayimg.com/kq/.../Bonn.Garcia-Moreno.Fjeldsa.pdfGuillett, A. M.
- Gonçalves, P.R., Myers, P., Vilela, J.F. & Oliveira, J.A. (2007). Systematics of species of the genus *Akodon* (Rodentia: Sigmodontinae) in southeastern Brazil and implications for the biogeography of the campos de altitude. *Miscellaneous Publications Museum of Zoology University of Michigan*, 197, 1–24. <https://ufrij.academia.edu/PabloGon%C3%A7alves>, accessed 19 September 2014.
- Gontijo, B.M. (2008). Uma geografia para a Cadeia do Espinhaço [A geography for the Espinhaço Range]. *Megadiversidade*, 4, 7–15. <http://www.conservation.org.br/publicacoes/megadiversidade04.php>, accessed 19 September 2014.
- Gonzaga, L.P. (2001). *Análise Filogenética do Gênero Formicivora Swainson 1825 (Aves: Passeriformes: Thamnophilidae) Baseada em Caracteres Morfológicos e Vocais [Phylogenetic Analysis of the Genus Formicivora Swainson 1825 (Aves: Passeriformes: Thamnophilidae) Based on Morphological Characters and Vocals]* (Unpublished doctoral dissertation). Universidade Federal do Rio de Janeiro, Rio de Janeiro.
- Gonzaga, L.P., Carvalhaes, A.M.P. & Buzzetti, D.R.C. (2007). A new species of *Formicivora* antwren from the Chapada Diamantina, eastern Brazil (Aves: Passeriformes: Thamnophilidae). *Zootaxa*, 1473, 25–44. <http://www.scribciolo.com/Formicivora%20grantsau%20Zootaxa%201473.pdf>, accessed 19 September 2014.
- Gould, J. (1861). *A monograph of the Trochilidae, or family of humming-birds*, Vol. 3. Taylor and Francis, London, <http://www.biodiversitylibrary.org/bibliography/51056#/summary>, accessed 19 September 2014.
- Guillett, A.M., Pirani, J.R., & Harley, R.M. (1997). Espinhaço Range region, eastern Brazil. In: S.D. Davis, V.H. Heywood, O. Herrera-Macbride, J. Villa-Lobos, & A.C. Hamilton (Eds.), *Centres of plant diversity: a guide and strategy for their conservation* (pp. 397–404). Oxford: Oxford Information Press.
- Habel, J.C. & Assmann, T., Eds. (2010). *Relict species. Phylogeography and Conservation Biology*. London: Springer. doi: 10.1007/978-3-540-92160-8_2
- Haffer, J. (1974). *Avian speciation in South America*. Cambridge: Nuttall Ornithological Club.
- Harley, R.M. (1995). Introduction. In: B.L. Stannard, & Y.B. Harvey, (Eds.), *Flora of the Pico das Almas, Chapada Diamantina – Bahia, Brazil* (pp. 1–42). Kew: Royal Botanic Gardens.
- Hosner, P.A. & Moyle, R.G. (2012). A Molecular Phylogeny of Black-Tyrants (Tyrannidae: *Knipolegus*) Reveals Strong Geographic Patterns and Homoplasy in Plumage and Display Behavior. *The Auk*, 129, 156–167. doi: 10.1525/auk.2012.11101
- Irestedt, M., Fjeldså, J., Johansson, U.S. & Ericson, P.G.P. (2002). Systematic relationships and biogeography of the tracheophone suboscines (Aves: Passeriformes). *Molecular Phylogenetics and Evolution*, 23, 499–512. doi: 10.1016/S1055-7903(02)00034-9
- Iriondo, M. & García, N. (1993). Climatic variations in the Argentine plains during the last 18,000 years. *Palaeoecology, Paleoclimatology, Palaeoecology*, 101, 209–220. doi: 10.1016/0031-0182(93)90013-9

- Klicka, J., Burns, K. & Spellman, G.M. (2007). Defining a monophyletic Cardinalini: A molecular perspective. *Molecular Phylogenetics and Evolution*, *45*, 1014–1032. doi: 10.1016/j.ympev.2007.07.006
- Leite, F.S.F., Juncá, F.A. & Eterovick, P.C. (2008). Status do conhecimento, endemismo e conservação de anfíbios anuros da Serra do Espinhaço, Brasil [Status of knowledge, endemism and conservation of amphibians of the Serra do Espinhaço, Brazil]. *Megadiversidade*, *4*, 182–200. <http://www.conservation.org.br/publicacoes/megadiversidade04.php>, accessed 19 September 2014.
- Lencioni-Neto, F. (1996). Uma nova subespécie de *Knipolegus* (Aves, Tyrannidae) do estado da Bahia, Brasil [A new subspecies of *Knipolegus* (Aves, Tyrannidae) in the state of Bahia, Brazil]. *Revista Brasileira de Biologia*, *56*, 197–201.
- Longhi-Wagner, H.M., Welker, C.A.D. & Waechter, J.L. (2012). Floristic affinities in montane grasslands in eastern Brazil. *Systematics and Biodiversity*, *10*, 537–550. doi: 10.1080/14772000.2012.753487
- Lousada, J.M., Borba, E.L. & Lovato, M.B. (2011). Genetic structure and variability of the endemic and vulnerable *Vellozia gigantea* (Velloziaceae) associated with the landscape in the Espinhaço Range, in southeastern Brazil: implications for conservation. *Genetica*, *139*, 431–440. doi: 10.1007/s10709-011-9561-5
- Lousada, J.M., Lovato, M.B. & Borba, E.L. (2013). High genetic divergence and low genetic variability in disjunct populations of the endemic *Vellozia compacta* (Velloziaceae) occurring in two edaphic environments of Brazilian *campos rupestres*. *Brazilian Journal of Botany*, *36*, 45–53. doi: 10.1007/s40415-013-0001-x
- Manel, S., Schwartz, M.K., Luikart, G. & Taberlet, P. (2003). Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology & Evolution*, *18*, 189–197. doi: 10.1016/S0169-5347(03)00008-9
- Martinelli, G. (2007). Mountain biodiversity in Brazil. *Revista Brasileira de Botânica*, *30*, 587–597. doi: 10.1590/S0100-84042007000400005
- Mata, H., Fontana, C.S., Maurício, G.N., Bornschein, M.R., Vasconcelos, M.F. & Bonatto, S. L. (2009). Molecular phylogeny and biogeography of the eastern tapaculos (Aves: Rhinocryptidae: *Scytalopus*, *Eleoscytalopus*): cryptic diversification in Brazilian Atlantic Forest. *Molecular Phylogenetics and Evolution*, *53*, 450–462. doi: 10.1016/j.ympev.2009.07.017
- Maurício, G.N. (2005). Taxonomy of southern populations in the *Scytalopus speluncae* group, with description of a new species and remarks on the systematics and biogeography of the complex (Passeriformes: Rhinocryptidae). *Revista Brasileira de Ornitologia*, *13*, 7–28. <http://www4.museu-goeldi.br/revistabronito/revista/index.php/BJO/article/view/2101>, accessed 19 September 2014.
- Mcguire, J.A., Witt, C.C., Altshuler, D.L. & Remsen, J.V.Jr. (2007). Phylogenetic systematics and biogeography of hummingbirds: Bayesian and maximum likelihood analyses of partitioned data and selection of an appropriate partitioning strategy. *Systematic Biology*, *56*, 837–856. doi: 10.1080/10635150701656360
- Mcguire, J.A., Witt, C.C., Remsen, J.V.Jr., Dudley, R. & Altshuler, D.L. (2009). A higher-level taxonomy for hummingbirds. *Journal of Ornithology*, *150*, 155–165. doi: 10.1007/s10336-008-0330-x
- Mcguire, J.A., Witt, C.C., Remsen, J.V.Jr., Corl, A., Rabosky, D.L., Altshuler, D.L. & Dudley, R. (2014). Molecular Phylogenetics and the Diversification of Hummingbirds. *Current Biology*, *24*, 910–916. doi: 10.1016/j.cub.2014.03.016
- Melo-Júnior, T.A., Vasconcelos, M.F., Fernandes, G.W. & Marini, M.A. (2001). Bird species distribution and conservation in Serra do Cipó, Minas Gerais, Brazil. *Bird Conservation International*, *11*, 189–204.
- Mello-Silva, R. (2010). Circumscribing *Vellozia hirsuta* and *V. tubiflora* (Velloziaceae). *Hoehnea*, *37*, 617–646. doi: 10.1590/S2236-89062010000300009
- Ohlson, J., Fjeldså, J. & Ericson, P.G.P. (2008). Tyrant flycatchers coming out in the open: phylogeny and ecological radiation of Tyrannidae (Aves, Passeriformes). *Zoologica Scripta*, *37*, 315–335. doi: 10.1111/j.1463-6409.2008.00325.x
- Ohlson, J., Irestedt, M., Ericson, P.G.P. & Fjeldså, J. (2013). Phylogeny and classification of the New World suboscines (Aves, Passeriformes). *Zootaxa*, *3613*, 001–035. doi: 10.11646/zootaxa.3613.1.1
- Ortiz-Jaureguizar, E. & Cladera, G.A. (2006). Paleoenvironmental evolution of southern South America during the Cenozoic. *Journal of Arid Environments*, *66*, 498–532. doi: 10.1016/j.jaridenv.2006.01.007
- Parrini, R., Raposo, M.A., Pacheco, J.F., Carvalhães, A.M.P., Melo-Júnior, T.A., Fonseca, P.S.M. & Minns, J.C. (1999). Birds of the Chapada Diamantina, Bahia, Brazil. *Cotinga*, *11*, 86–95. <http://www.neotropicalbirdclub.org/articles/11/c11-diaman.pdf>, accessed 19 September 2014.
- Petri, S. & Fúlfar, V.J. (1983). *Geologia do Brasil (Fanerozoico) [Geology of Brazil (Phanerozoic)]*. Sao Paulo: Editora USP.
- Pirani, J.R. & Harley, R.M. (1997). Espinhaço Range region, eastern Brazil. In: S. D. Davis, V. H. Heywood, O. Herrera-Macbride, J. Villa-Lobos, & A. C. Hamilton (Eds.) *Centres of plant diversity: a guide and strategy for their conservation* (pp. 397–404). Oxford: Oxford Information Press. pp. 397–404.
- Prado, D.E. (2000). Seasonally dry forests of tropical South America: from forgotten ecosystems to a new phyto-geographic unit. *Edinburgh Journal of Botany*, *57*, 437–461.
- Quintero, E., Ribas, C.C. & Cracraft, J. (2012). The Andean *Hapalopsittaca* parrots (Psittacidae, Aves): an example of montane-tropical lowland vicariance. *Zoologica Scripta*, *42*, 28–43. doi: 10.1111/j.1463-6409.2012.00567.x
- Rabassa, J., Coronato, A.M. & Salemme, M. (2005). Chronology of the Late Cenozoic Patagonian glaciations and their correlation with biostratigraphic units of the Pampean region (Argentina). *The Journal of South American Earth Sciences*, *20*, 81–103. doi: 10.1016/j.jsames.2005.07.004
- Rapini, A., Ribeiro, P.L., Lambert, S. & Pirani, J.R. (2008). A flora dos campos rupestres da Cadeia do Espinhaço [The flora of the campos rupestres of the Espinhaço Range]. *Megadiversidade*, *4*, 15–23. <http://www.conservation.org.br/publicacoes/megadiversidade04.php>, accessed 19 September 2014.
- Remsen, J.V.Jr. (2003). Family Furnariidae (Ovenbirds). In: J. Del Hoyo, A. Elliot, & D.A., Christie (Eds.), *Handbook of the Birds of the World*, Vol. 8, (pp. 162–357). Cambridge and Barcelona: BirdLife International and Lynx Editions.
- Rheindt, F.E., Norman, J.A. & Christidis, L. (2008). Phylogenetic relationships of tyrant-flycatchers (Aves: Tyrannidae), with an emphasis on the elaeiniine assemblage. *Molecular Phylogenetics and Evolution*, *46*, 88–101. doi: 10.1016/j.ympev.2007.09.011
- Ribas, C.C., Moyle, R.G., Miyaki, C.Y. & Cracraft, J. (2007). The assembly of montane biotas: linking Andean tectonics

- and climatic oscillations to independent regimes of diversification in *Pionus* parrots. *Proceedings of the Royal Society B*, 274, 2399–2408. doi: 10.1098/rspb.2007.0613
- Rodrigues, M.T.U. (2008). *Placosoma* cipoense Cunha, 1966. In: A.B.M. Machado, G.M. Drummond, & A.P. Paglia (Eds.), *Livro Vermelho da Fauna Brasileira Ameaçada de Extinção [Red List of Brazilian Fauna Threatened of Extinction]* (pp. 336–337). Brasília and Belo Horizonte: Ministério do Meio Ambiente and Fundação Biodiversitas.
- Rodrigues, M., Freitas, G.H.S., Costa, L.M., Dias, D.F., Varela, M.L.M. & Rodrigues, L.C. (2011). Avifauna, Alto do Palácio, Serra do Cipó National Park, state of Minas Gerais, southeastern Brazil. *Check List*, 7, 151–161. <http://www.checklist.org.br/getpdf?SL067-10>, accessed 19 September 2014.
- Saadi, A. (1995). A geomorfologia da Serra do Espinhaço em Minas Gerais e de suas margens [The geomorphology of the Serra do Espinhaço in Minas Gerais and its margins]. *Geonomos*, 3, 41–63. http://www.igc.ufmg.br/geonomos/PDFs/3_1_41_63_Saadi.pdf, accessed 19 September 2014.
- Safford, H.D. (1999). Brazilian Páramos I. An introduction to the physical environment and vegetation of the campos de altitude. *Journal of Biogeography*, 26, 693–712. doi: 10.1046/j.1365-2699.1999.00313.x
- Safford, H.D. (2007). Brazilian Páramos IV. Phytogeography of the campos de altitude. *Journal of Biogeography*, 34, 1701–1722. doi: 10.1111/j.1365-2699.2007.01732.x
- Salino, A. & Almeida, T.E. (2008). Diversidade e conservação das pteridófitas na Cadeia do Espinhaço, Brasil [Diversity and conservation of pteridophytes in the Espinhaço Range, Brazil]. *Megadiversidade*, 4, 50–70. <http://www.conservation.org.br/publicacoes/megadiversidade04.php>, accessed 19 September 2014.
- Sánchez-Barcaldo, P. (2004). Phylogenetics and biogeography of the Neotropical fern genera *Jamesonia* and *Eriosorus* (Pteridaceae). *The American Journal of Botany*, 91, 274. doi: 10.3732/ajb.91.2.274
- Sanín, C., Cadena, C.D., Maley, J.M., Lijtmaer, D.A., Tubaro, P. L. & Chesser, R.T. (2009). Paraphyly of *Cincludes fuscus* (Aves: Passeriformes: Furnariidae): implications for taxonomy and biogeography. *Molecular Phylogenetics and Evolution*, 53, 547–555. doi: 10.1016/j.ympev.2009.06.022
- Schuchmann, K.L. (1999). Family Trochilidae (Hummingbirds). In: J. Del Hoyo, A. Elliot, & J. Sargatal (Eds.), *Handbook of the Birds of the World: Barn-owls to hummingbirds*, Vol. 5 (pp. 468–680). Barcelona: Lynx Edicions.
- Sibley, C.G. & Monroe, B.L.Jr. (1990). *Distribution and taxonomy of birds of the World*. New Haven: Yale University Press.
- Sick, H. (1970). Der Strohschwanz, *Oreophylax moreirae*, Andiner Furnariidae in Südostbrasilien [The Oreophylax moreirae, Andean Furnariidae in Southeastern Brazil]. *Bonner Zoologische Beiträge*, 21, 251–268.
- Sick, H. (1973). Nova contribuição ao conhecimento de *Cincludes pabsti* Sick, 1969 (Furnariidae, Aves) [New contribution to the knowledge of *Cincludes pabsti* Sick, 1969 (Furnariidae, Aves)]. *Revista Brasileira de Biologia*, 33, 109–117.
- Sick, H. (1985). Observations on the Andean-Patagonian component of Southeastern Brazil's avifauna. *Ornithological Monographs*, 36, 233–237. <http://www.jstor.org/stable/40168284>, accessed 19 September 2014.
- Sick, H. (1997). *Ornitologia brasileira*. Rio de Janeiro: Nova Fronteira.
- Silva, J.M.C. (1995). Biogeographic analysis of the South American Cerrado avifauna. *Steenstrupia*, 21, 49–67.
- Silva, J.M.C. (1997). Endemic bird species and conservation in the Cerrado region, South America. *Biodiversity and Conservation*, 6, 435–450. doi: 10.1023/A:1018368809116
- Silva, J.M.C. & Bates, J.M. (2002). Biogeographic patterns and conservation in the South American Cerrado: a tropical savanna hotspot. *BioScience*, 52, 225–233. doi: 10.1641/0006-3568(2002)052[0225:BPACIT]2.0.CO;2
- Silveira, F.A. & Cure, J.R. (1993). High-altitude bee fauna of southeastern Brazil: implications for biogeographic patterns (Hymenoptera: Apoidea). *Studies on Neotropical Fauna and Environment*, 28, 47–55. doi: 10.1080/01650529309360887
- Simpson, B.B. (1979). Quaternary biogeography of the high montane regions of South America. In: W.E. Duellman (Ed.), *The South American herpetofauna: its origin, evolution, and dispersal* (pp. 157–188). Lawrence: University of Kansas.
- Simpson-Vuilleumier, B. (1971). Pleistocene changes in the fauna and flora of South America. *Science*, 173, 771–780. doi: 10.1126/science.173.3999.771
- Struwe, L., Haag, S., Heiberg, E. & Grant, J.R. (2009). Andean speciation and vicariance in Neotropical Macrocarpaea (Gentianaceae–Helieae). *Annals of the Missouri Botanical Garden*, 96, 450–469. doi: 10.3417/2008040
- Tello, J.G., Moyle, R.G., Marchese, D.J. & Cracraft, J. (2009). Phylogeny and phylogenetic classification of the tyrant flycatchers, cotingas, manakins, and their allies (Aves: Tyrannidae). *Cladistics*, 25, 1–39. doi: 10.1111/j.1096-0031.2009.00254.x
- UNESCO. (2005). *MAB Biosphere reserves directory*. Retrieved from <http://www.brasilia.unesco.org/noticias/releases/2005/biosferaespinhaco>, accessed 19 September 2014.
- Uzzell, T.M.Jr. (1959). Teiid lizards of genus *Placosoma*. *Occasional papers of the Museum of Zoology, University of Michigan*, 606, 1–15. <http://deepblue.lib.umich.edu/handle/2027.42/57043>, accessed 19 September 2014.
- Vanzolini, P.E. (1963). *Problemas faunísticos do Cerrado [Faunistic problems of Cerrado]*. In: Simpósio sobre o Cerrado. M. Ferri (Ed.). Editora da Universidade de São Paulo, São Paulo.
- Vasconcelos, M.F. (2008). Mountaintop endemism in eastern Brazil: Why some bird species from campos rupestres of the Espinhaço Range are not endemic to the Cerrado region? *Revista Brasileira de Ornitologia*, 16, 348–362. http://www4.museu-goeldi.br/revistabromito/revista/index.php/BJO/article/view/5206/pdf_821, accessed 19 September 2014.
- Vasconcelos, M.F. (2011). O que são campos rupestres e campos de altitude nos topos de montanha do Leste do Brasil? [What are *campos rupestres* and *campos de altitude* in the mountaintops of eastern Brazil?]. *Revista Brasileira de Botânica*, 34, 241–246. <http://www.scielo.br/pdf/rbb/v34n2/a12v34n2.pdf>, accessed 19 September 2014.
- Vasconcelos, M.F. & Melo-Júnior, T.A. (2001). An ornithological survey of Serra do Caraça, Minas Gerais, Brasil. *Cotinga*, 15, 21–31. <http://www.neotropicalbirdclub.org/pages/jmenu.asp?IssueID=15>, accessed 19 September 2014.
- Vasconcelos, M.F. & Pacheco, J.F. (2012). A contribuição histórica das atividades de coleta científica nos séculos XIX e XX para o conhecimento da avifauna dos campos rupestres e campos de altitude do leste brasileiro [The historical contribution of scientific collecting activities in the nineteenth and twentieth centuries to the knowledge of the avifauna of the *campos rupestres* and *campos de altitude* eastern Brazil]. *Atualidades Ornitológicas*, 168, 52–65. http://www.ao.com.br/download/AO168_52.pdf, accessed 19 September 2014.
- Vasconcelos, M.F. & Rodrigues, M. (2010). Patterns of biogeographic, distribution and conservation of the open-habitat avifauna of southeastern Brazilian mountaintops (*campos rupestres* and *campos de altitude*). *Papéis Avulsos de Zoologia*, 50, 1–29. doi: 10.1590/S0031-10492010000100001

- Vasconcelos, M.F., Lopes, E.L., Machado, C.G. & Rodrigues, M. 2008a. As aves dos campos rupestres da Cadeia do Espinhaço: diversidade, endemismo e conservação [The birds of campos rupestres of the Espinhaço: diversity, endemism and conservation]. *Megadiversidade*, 4, 221–241. <http://www.conservation.org.br/publicacoes/megadiversidade04.php>, accessed 19 September 2014.
- Vasconcelos, M.F., Maldonado-Coelho, M. & Buzzetti, D.R.C. (2003). Range extensions for the Gray-backed Tachuri (*Polystictus superciliaris*) and the Pale-throated Sierra-finch (*Embernagra longicauda*) with a revision on their geographic distribution. *Ornitologia Neotropical*, 14, 477–489. <https://sora.unm.edu/sites/default/files/journals/on/v014n04/p0477-p0490.pdf>, accessed 19 September 2014.
- Vasconcelos, M.F., Chaves, A.V. & Santos, F.R. (2012). First record of *Augastes scutatus* for Bahia refines the location of a purported barrier promoting speciation in the Espinhaço Range, Brazil. *Revista Brasileira de Ornitologia*, 20, 443–446. http://www4.museu-goeldi.br/revistabornito/revista/index.php/BJO/article/viewFile/0249/pdf_645, accessed 19 September 2014.
- Versieux, L.M., Wendt, T., Louzada, R.B. & Wanderley, M.G.L. (2008). Bromeliaceae da Cadeia do Espinhaço. *Megadiversidade*, 4, 98–110. <http://www.conservation.org.br/publicacoes/megadiversidade04.php>, accessed 19 September 2014.
- Vianna, P.L. & Filgueiras, T.S. (2008). Inventário e distribuição geográfica das gramíneas (Poaceae) na Cadeia do Espinhaço, Brasil [Inventory and geographical distribution of grasses (Poaceae) in the Espinhaço Range, Brazil]. *Megadiversidade*, 4, 71–88. <http://www.conservation.org.br/publicacoes/megadiversidade04.php>, accessed 19 September 2014.
- Vielliard, J.M.E. 1990a. Estudo bioacústico das aves do Brasil: o gênero *Scytalopus* [Bioacoustic study of the birds of Brazil: *Scytalopus* genus]. *Ararajuba*, 1, 5–18.
- Vielliard, J.M.E. 1990b. Uma nova espécie de *Asthenes* da Serra do Cipó, Minas Gerais, Brasil [A new species of *Asthenes* Serra do Cipo, Minas Gerais, Brazil]. *Ararajuba*, 1, 121–122.
- Werneck, F.P., Costa, G.C., Colli, G.R., Prado, D.E. & Sites, J. W.Jr. (2011). Revisiting the historical distribution of Seasonally Dry Tropical Forests: new insights based on palaeo-distribution modelling and palynological evidence. *Global Ecology and Biogeography*, 20, 272–288. doi: 10.1111/j.1466-8238.2010.00596.x
- Willis, E.O. (1992). Zoogeographical origins of eastern Brazilian birds. *Ornitologia Neotropical*, 3, 1–15. http://www.ibiologia.unam.mx/pdf/links/neo/rev3/vol_3_1/ornitol%203_1_1_15.pdf, accessed 19 September 2014.
- Whitney, B.M., Vasconcelos, M.F., Silveira, L.F. & Pacheco, J. F. (2010). *Scytalopus petrophilus* (Rock Tapaculo): a new species from Minas Gerais, Brazil. *Revista Brasileira de Ornitologia*, 18, 73–88. http://www4.museu-goeldi.br/revistabornito/revista/index.php/BJO/article/view/3901/pdf_748, accessed 19 September 2014.
- Zanella, F.C.V. (2011). Evolução da Biota da Diagonal de Formações Abertas secas da América do Sul [Evolution of Diagonal Open Formations Biota droughts in South America]. In: C.J.B. Carvalho, & E.A.B. Almeida (Eds.), *Biogeografia da América do Sul; padrões e processos [Biogeography of South America: standards and procedures]* (pp. 198–220). São Paulo: Editora Roca.
- Zimmer, K. & Isler, M.L. (2003). Family Thamnophilidae. In: J. Del Hoyo, A. Elliot, & D.A. Christie (Eds.), *Handbook of the Birds of the World*, Vol. 8 (pp. 358–447). Barcelona: Lynx Editions.

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