Areas of endemism for passerine birds in the Atlantic forest, South America

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ABSTRACT

Aim To use the method of parsimony analysis of endemism to identify areas of endemism for passerine birds in the Atlantic Forest, South America, and to compare the locations of these areas with areas previously identified for birds as well as other taxa.

Location The Atlantic Forest, eastern South America.

Methods We analysed a matrix composed of the presence (1) or absence (0) of 140 endemic species in 24 quadrats of 1 × 1 degree distributed along the Atlantic Forest to find the most parsimonious area cladogram.

Results Fourteen most parsimonious cladograms were found and then summarized in a single consensus tree. Four areas of endemism were identified: Pernambuco, Central Bahia, Coastal Bahia, and Serra do Mar.

Main conclusions Avian areas of endemism in the Atlantic Forest have significant generality, as they are highly nonrandom and congruent with those of other groups of organisms. A first hypothesis about the historical relationships among the four areas of avian endemism in the Atlantic Forest is delineated. There is a basal dichotomy among areas of endemism in the Atlantic Forest, with Pernambuco forming a northern cluster and Coastal Bahia, Central Bahia and Serra do Mar comprising a southern cluster. Within the southern cluster, Central Bahia and Serra do Mar are more closely related to each other than to Coastal Bahia.

Keywords Areas of endemism, Atlantic Forest, biogeography, Brazil, evolution, Neotropics, passerine birds, phylogeny.

INTRODUCTION

Two basic patterns of geographical distribution are recognized in biogeography (Brown & Lomolino, 1998). The first is that geographical distributions of organisms are limited by ecological or historical factors; thus no taxon is completely cosmopolitan but many are endemic to restricted regions. The second pattern is that endemic species are not distributed randomly but they tend to be concentrated in some regions of the world, constituting a phenomenon called provincialism.

Regions with at least two endemic taxa are named areas of endemism (Cracraft, 1985; Platnick, 1991). They are important for two reasons. The first is that they represent the smallest geographical units of analysis in historical biogeography, forming the base for postulating hypotheses about the history of geographical units and their biotas (Cracraft, 1985, 1994; Morrone, 1994; Morrone & Crisci, 1995). The second is that areas of endemism harbour unique biotas and therefore are considered as priority targets for conservation action (Terborgh & Winter, 1982; Fjeldså, 1993).

There are several methods used to identify areas of endemism at a continental scale. The method more commonly used consists of superimposing distribution maps for a number of taxa to identify areas characterized by high concentrations of overlapping ranges (Müller, 1973). However, the overlap among species’ ranges may not be perfect and arbitrary decisions are taken when a great number of species are analysed (Platnick, 1991; Silva & Oren, 1996).

Recently, a new method was proposed to identify areas of endemism (Morrone, 1994). The method applies a parsimony algorithm (commonly used in phylogenetic analyses) on matrices with the raw distributions of organisms to identify areas or sets of areas that share a unique group of endemic taxa. This method presents several advantages compared to the traditional
method. It is clearer, direct and can easily be improved when more information on geographical distribution becomes available (Posadas & Miranda-Esquivel, 1999).

The Atlantic Forest is one of the best defined biogeographical regions in South America. From a continental perspective, the Atlantic Forest can be considered an island, because it is isolated from other large blocks of South American forests (Amazonian and Andean forests) by a corridor of semiopen formations, comprising Caatinga, Cerrado and Chaco (Ab’Saber, 1977). Due to this isolation, the Atlantic Forest harbours a unique biota with many endemic genera and species (Myers et al., 2000).

The Atlantic Forest, however, is not homogeneous. Several factors contribute to the environmental diversity of this region. One is the latitudinal range, of about 25 degrees, thus including different climatic regimes (Nimer, 1979). Another relevant factor is altitude, as forests cover areas from sea level to 1700 m a.s.l. (Rizzini, 1997). Latitude and altitude together produce conditions for the development of distinctive types of vegetation (Hueck, 1972; Rizzini, 1997). This, in turn, influences species’ distributions (Brown & Lomolino, 1998).

Several attempts have been made to identify avian areas of endemism in the Atlantic Forest. Although using the traditional methods, their results differed in several aspects. Müller (1973) analysed several terrestrial vertebrates’ ranges (including several bird species) and considered the Atlantic Forest as a single area of endemism. However, he identified at least three subareas of endemism: Pernambuco, Bahia and Paulista. Cracraft (1985) identified two areas of endemism for birds along the Atlantic Forest: Serra do Mar, which stretches from Pernambuco to Santa Catarina along the coastal zone; and Paraná, which encompasses the region covered by Araucaria forests in southern Brazil. Haffer (1985) regarded the Atlantic Forest as a single area of endemism, named South-eastern Brazil. Stattersfield et al. (1998) identified five avian areas of endemism in eastern Brazil: the Atlantic Slope of Alagoas and Pernambuco; Deciduous forests of Bahia; Deciduous forests of Minas Gerais and Goiás; Atlantic Forest lowlands; and Atlantic Forest mountains.

This paper has three main goals. The first is to use Morrone’s methodology to identify areas of endemism along the Atlantic Forest using passerine birds as a study group. The second is to evaluate the generality of the areas identified using this method by comparing them with those identified for other organisms. The final goal is to use the area cladogram generated in the analysis to propose, for the first time, a general hypothesis of historical relationships among areas of endemism of the Atlantic Forest.

METHODS

Study area

About 95% of the Atlantic Forest lies in Brazil, the remainder in Argentina and Paraguay. The core region of Atlantic Forest corresponds to an almost continuous zone composed of several forest types along the Brazilian coast, from Rio Grande do Norte to Rio Grande do Sul (Fig. 1). In addition, other disjunct regions are currently also considered as Atlantic Forest (Conservation International et al., 2000): (a) evergreen to semideciduous forest islands (regionally known as ‘brejos’) located in the slopes of residual plateaus in the Caatinga region; (b) deciduous and semi-isolated forests along the middle section of the São Francisco river and in southern Piauí; and (c) deciduous and semideciduous forests isolated along the Serra da Bodoquena, Mato Grosso do Sul. In total, this area corresponds to about 1,400,000 km².

Identification of areas of endemism

The method proposed by Morrone (1994) comprises the following steps: (a) define operational geographical unites (OGU); (b) construct a data matrix; (c) perform a parsimony analysis of the data matrix; (d) delimit the OGU or groups of OGUs defined by at least two endemic species; and (e) map the species endemic to each OGU or groups of OGUs to delineate the boundaries of each area of endemism.

Sample localities are the ideal OGUs for the parsimony analysis of distribution data (Rosen, 1988), however, our knowledge of the geographical distribution of bird species along the Atlantic Forest is incomplete as several places have not been adequately sampled for birds (Conservation International et al., 2000). To circumvent this problem, several authors have used as OGUs a previous regionalization scheme, such as provinces, districts, interfluvial regions, or ecoregions (Cracraft, 1991, 1994; Silva & Oren, 1996; Morrone & Escalante, 2002). However, Silva & Oren (1995) pointed out that this strategy is based on a critical assumption, namely that the biotic difference within an OGU is smaller than among OGUs. We used a different approach. We selected 24 quadrats of 1 × 1 degree, which together cover most of the Atlantic Forest (Fig. 1). These quadrats were selected based on two criteria. The first (‘sampling criterion’) is that each quadrat must have at least one or a set of localities that have been reasonably sampled for birds. The second criterion (‘representation criterion’) is that these quadrats must collectively encompass the major forest types (according to the IBGE, 1988) and latitudinal belts of the Atlantic Forest.

The endemic passerine species of the Atlantic Forest were selected from a list presented by Pacheco & Bauer (1999). Then, the general distribution and ecological requirements of each species were separately re-evaluated to confirm that species were endemic to the region and also restricted to forest environments. As a result, some species (Formicivora serrana, Oreophaia moreirae, Elaenia ridleyana, Vireo gracilirostris, Hylophilus poiclolitis, Euphonia pectoralis, Sporophila melanogaster) listed as endemic by Pacheco & Bauer (1999) were excluded from the final list of species, whereas others (Leptidocolaptes wagleri, Lepidocolaptes squamatus, Arremon franciscanus and Phylloscartes roquettei) were included. Species’ ranges were obtained from several sources, such as books (Pinto et al. 1978; Ridgely & Tudor, 1994, 1997; Sick, 1997), papers on systematics and distribution (Bornschein et al., 1995, 1998, 2001; Gonzaga & Pacheco, 1995; Gonzaga et al., 1995; Pacheco & Gonzaga, 1995; Whitney et al., 1995a,b; Silva & Straube, 1996; Isler et al., 1997; Pacheco, 1997; Raposo, 1997; Whitney & Pacheco, 1997; Willis, 1988), regional/
Bird areas of endemism in the Atlantic Forest

One hundred and forty species of endemic passerines were included in this analysis (Appendix 1). Fourteen most parsimonious cladograms were found. Thus, a strict consensus cladogram was generated to identify unambiguous clusters of OGUs (Fig. 2). Four areas of endemism may be identified from this analysis. The first area is composed of quadrat A, defined by six species (*Myrmotherula snowi*, *Terenura sicki*, *Synallaxis infuscata*, *Philydor novaesi*, *Phylloscartes ceciliae* and *Tangara fastuosa*). The second area is composed of quadrats D and E, and is defined by four endemic species (*Synallaxis cinerea*, *Phylloscartes beckeri*, *Rhopornis ardesiaca* and *Formicivora iheringi*). The third area is composed only of quadrat F, and is defined by two species (*Acroboratornis fonsecai* and *Scytalopus psychopompus*). The fourth area of endemism is composed of quadrats Q, U, J, V, S, R, P, M and N. This area is defined by two species (*Orthogonys chloricterus* and *Dacnis nigripes*). When compared with all other areas of endemism identified, the fourth area is the only one in which nested subareas of endemism may be also recognized. Thus, the subcluster composed of quadrats U, J, V, S, R, P, M and N is defined by two species (*Myrmotherula gularis* and *Tangara desmarestii*); the subcluster S, R, P, M and N is defined by two species (*Biatas nigropectus* and *Drymophila rubricollis*); and quadrat N is defined by four species (*Myrmotherula fluminensis*, *Formicivora

**RESULTS**

Figure 1 The Atlantic Forest in eastern South America. A set of 24 quadrats was selected to cover most of the environmental variation that there is in this biome.
littoralis, Tijuca condita and Calyptura cristata). By combining the ranges of the endemic species listed above, it is possible to delimit four areas of endemism (Fig. 3): Pernambuco (A), Central Bahia (D and E), Coastal Bahia (F), and Serra do Mar (Q, U, J, V, S, R, P, M, and N).

Pernambuco includes all evergreen, semideciduous and deciduous forests that are orientated as a belt following the Atlantic coast, north to the river São Francisco. It comprises the coastal zone of the states of Paraíba, Pernambuco and Alagoas. Central Bahia includes a large and topographically complex area that harbours a mosaic of evergreen, semideciduous and deciduous forests, which cover both slopes and adjacent areas of the Chapada da Diamantina and all surrounding plateaus in central Bahia and northern Minas Gerais. Coastal Bahia encompasses a small area dominated by lowland evergreen forests roughly between the rivers Jequitinhonha and Jequitinhonha, in the state of Bahia. Serra do Mar includes a very heterogeneous habitat gradient that ranges from coastal restingsas at sea level to forests at 1700 m a.s.l. This area follows roughly the belt of high-elevation ranges that is generally named 'Serra do Mar' and that extends from central Espírito Santo to Santa Catarina.

**DISCUSSION**

**Avian areas of endemism**

The analysis indicates that there are distinct areas of passerine bird endemism in the Atlantic Forest. Four distinctive and basal areas of endemism were identified and they form the base upon which a systematic research program on avian biogeography in this region may be developed. This result supports the prediction by Cracraft (1985) that his 'Serra do Mar Centre' would be subdivided into smaller areas of endemism when bird distributions were examined in more detail.

The identification of the four areas of endemism differs from previous analyses. In contrast with Müller (1973), the area of endemism Pernambuco does not include both banks of the river São Francisco, because all endemic bird species that delimit this region are restricted to the northern bank. Also, Müller's Bahia subcentre does not strictly follow the Atlantic coast. Finally, although Müller's Paulista subcentre is largely congruent with the area of endemism Serra do Mar, it does not extend up to Espírito Santo.

In contrast with Cracraft (1985), we could not find any support for the Paraná Centre (encompassing central Paraná, western Santa Catarina and northern Rio Grande do Sul) as an area of endemism. Cracraft listed 12 bird taxa as supporting the Paraná Centre, including six passerine species: five forest specialists (Clibanornis dendrocolaptoides, Leptasthenura setaria, Leptasthenura striolata, Hemitriccus kaempferi, Cyanocorax caeruleus), and one grassland specialist (Anthus nattereri). The ranges of these species are not restricted to Paraná Centre (see Appendix 1) and include also other areas of endemism. In fact, our analysis suggests that at least the eastern portion of Cracraft's Paraná Centre (quadra Q in Fig. 2) is part of the area of endemism Serra do Mar, whilst other sectors (quarters T, X and Z) comprise a transition zone with other biomes.

Stattersfield *et al.* (1998) recognized only one of the areas of endemism that we identified: Pernambuco (they named this area as ’Atlantic slope of Alagoas and Pernambuco’). They also identified an area in central Bahia (’Deciduous forests of Bahia’), but their area is smaller and does not encompass the ranges of all species that we suggest are endemic to this region. Bird species that define the area of endemism Central Bahia inhabit different habitats. Two species (Synallaxis cinerea and Phylloscartes beckeri) are restricted to evergreen forests along the slopes of some high plateaus while Rhopornis ardesiaca and Formicivora iheringi are restricted to dry forests that surround these plateaus. Cracraft (1985) stressed that there is no reason to expect that endemic species defining an area of endemism (a primarily historical entity) should have the same ecological requirements. In addition, although these four species are not syntopic, they are sympatric at the spatial scale analysed herein and their ranges coincide spatially to define an area of endemism. Stattersfield *et al.* (1998) recognized one large area of endemism named ’Atlantic Forest lowlands’, which is largely congruent with the areas Coastal Bahia and Serra do Mar identified herein. They also identified an area of endemism named ’Atlantic Forest mountains’,...
pointing out that there are differences between lowland and highland avifaunas along the Serra do Mar. We could not find any evidence for this area of endemism and it is included in the Serra do Mar or in Central Bahia. We found no support to recognize Stattersfield’s area of endemism ‘Deciduous forests of Minas Gerais and Goiás’. This area of endemism is composed of two disjunct patches of dry forests (one in the São Francisco valley and another in the Paraná valley) separated by a large plateau covered mostly by cerrado. The ranges of the two species that they used to recognize this area of endemism are not fully coincident, because *Knipolegus franciscanus* occurs in both São Francisco and Paraná valleys, whilst *Phylloscartes roquettei* occurs only in the São Francisco valley.

**Comparison with areas of endemism of other organisms**

The four areas of endemism exhibit considerable congruence with those identified for other organisms in the Atlantic Forest. Prance (1982) identified three areas of endemism for woody plants (Pernambuco, Bahia and Rio de Janeiro) that are largely coincident with the areas identified herein (Pernambuco, Costal Bahia and Serra do Mar, respectively). Erwin & Pogue (1988) suggested that all coastal Atlantic Forest south of the river São Francisco is a single biogeographical unity that they named ‘South Atlantic Coast’. This scheme is not contradictory with the one suggested herein. Soderstrom *et al.* (1988) found two areas of endemism for bamboos along the Atlantic Forest. One (Bahia) is largely coincident with Coastal Bahia and another (Serra do Mar) is coincident with our area Serra do Mar. Tyler *et al.* (1994) identified four areas of endemism along the Atlantic Forest. Their area of endemism Pernambuco overlaps 100% with the Pernambuco area identified herein. Tyler *et al.*’s Bahia area includes a large extension of Coastal Bahia and a small portion of Central Bahia. Tyler *et al.*’s Rio de Janeiro and Santa Catarina areas are mostly included within the area of endemism Serra do Mar.

These comparisons indicate that passerine areas of endemism have significant generality, because endemic passerine species along the Atlantic Forest tend to cluster in the same regions as other groups of organisms. According to Cracraft (1985), this generality implies that there is a pattern to be investigated, namely, the origin and development of biotas as represented by these areas of endemism.

**Historical relationships among areas of endemism**

Although the analysis of species’ raw distributions using parsimony is effectively one good method to identify the areas of endemism at intracontinental scales (Silva & Oren, 1996; Posadas *et al.*, 1999; Garcia-Barros *et al.*, 2002; Morrone & Escalante, 2002), there are doubts if this method may be used to estimate historical relationships among areas of endemism (Brooks, 1981; McLennan & Brooks, 2002). Some authors claim that the results
from this method are congruent with those obtained using more sophisticated biogeographical analyses based on cladistic biogeography methods and on the phylogenies of different groups of species (e.g. Cracraft, 1991, 1994; Silva & Oren, 1995; Ron, 2000). Cracraft (1991) provided a rationale for this claim, by stating that shared taxa among areas may be evidence of historical relatedness, because they are the consequence of failure to differentiate once the areas became segregated. Cracraft (1994) also suggested that if biotic dispersion is historically constrained, it should be expected that the distribution of natural taxa will exhibit hierarchical congruence when examined cladistically. Silva & Oren (1995) suggested that the analysis of raw distributions of species using parsimony should be a useful tool to identify preliminary hypotheses of historical relationships among areas of endemism that may later be evaluated by the methods of cladistic biogeography.

Several authors have investigated the historical relationships of the Atlantic Forest with other lowland forest regions in South America (Cracraft & Prum, 1988; Bates, 1998; Costa et al., 2000). In all these broad-scale analyses, the hypothesis that the Atlantic Forest is a composite of at least two or more areas of endemism is well supported. The realization that the Atlantic Forest is composed of at least four areas of avian endemism will help refine those analyses and shed light on the complex issue of historical relationships among the areas of endemism in South America (Bates et al., 1998).

Recent studies indicate that most biotas are mosaics due to vicariance, peripheral isolates speciation, postspeciation dispersal, nonresponse to vicariance and extinction and that the same areas often have reticulated histories with respect to the species that live in them (McLennan & Brooks, 2002). Reticulated histories are in fact sets of different dichotomic relationships, each one representing a piece of the complex evolutionary history of a biota. The results obtained herein may be used to advance a first (but by no means the only) set of historical dichotomic relationships among areas of endemism for birds in the Atlantic Forest. The hypotheses derived from Fig. 2 are as follows: (a) there is a basal dichotomy among areas of endemism in the Atlantic Forest, with Pernambuco constituting a northern cluster, and Coastal Bahia, Central Bahia and Serra do Mar comprising a southern cluster; and (b) within the southern cluster, Central Bahia and Serra do Mar are more closely related to each other than to Coastal Bahia. This hypothesis may be tested by evaluating the phylogeny of monophyletic groups that have taxa (species or subspecies) endemic to at least three of these four areas of endemism. Three passerine groups could be good candidates for these tests. The first is Lepidocolaptes fuscus, because it is largely distributed in the Atlantic Forest and has a subspecies in each one of the areas of endemism: Pernambuco (atlanticus), Central Bahia (brevirostris), Coastal Bahia (tennirostris), and Serra do Mar (fuscus). The two other groups are also informative (Gonzaga & Pacheco, 1995; Pacheco & Gonzaga, 1995), but they lack species in Coastal Bahia: one is comprised of Synallaxis infuscata (Pernambuco), S. cinerea (Central Bahia), and S. ruficapilla (Serra do Mar); and the other is formed by Phylloscartes ceciliae (Pernambuco), P. beckeri (Central Bahia), and P. v. virescens (Serra do Mar).

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SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/GEB/GEB077/GEB077sm.htm

Appendix S1. Presence (1) and absence (0) of 140 endemic passerine endemic species in 24 quadrats in the Atlantic Forest. Lines are quadrats and columns are species. The line ‘root’ is an area with no taxon at all that is used to root the most parsimonious cladograms.

REFERENCES


**BIOSKETCHES**

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