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Historical relationships of areas of endemism of the Brazilian Atlantic rain forest: a cladistic biogeographic analysis of harvestman taxa (Arachnida: Opiliones)

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Abstract

Based on a cladistic biogeographic analysis of 6 species-level phylogenies of harvestman taxa, we searched for congruence in the historical relationships of 12 areas of endemism of the Brazilian Atlantic Rain Forest. We constructed general area cladograms using Primary Brooks Parsimony Analysis (BPA), BPA of nodes, and paralogy-free subtree analysis. These analyses resulted in 6 general area cladograms, that allow to infer a general pattern of the relationships among areas of endemism from the Brazilian Atlantic Rain Forest. Northern areas resulted related basally showing main disjunctions at the Doce River Valley and Todos os Santos Bay/São Francisco River Valley. The remaining areas of endemism were included in a southern and a southeastern block, separated by the Ribeira do Iguape Valley. Incongruence Length Differences tests showed no significant incongruence among the resulting cladograms and other matrix partitions. We concluded that tectonism and ancient marine transgressions were the probable processes responsible for the main disjunctions, whereas Neogene refugia seem to have caused the more recent disjunctions. The general pattern and redundancy in area relationships suggest a model of main reiterative barriers in diversification at multiple times for the evolution of the Atlantic Rain Forest. The renewal of cladistic biogeography and the search for common biogeographic patterns are discussed.

Key words: dispersal, historical biogeography, Mata Atlântica, speciation, vicariance.

Cladistic biogeography, originating in the 1970s, is a research program of historical or evolutionary biogeography which is aimed at inferring past area relationships based on the comparison of area cladograms of different taxa (Platnick and Nelson 1978; Rosen 1978; Wiley 1988; Humphries and Parenti 1999; Morrone 2009). In the last 20 years at least, biogeographic analyses of individual taxa based on molecular phylogenetic studies and models of nucleotide evolution have become increasingly more common, and the search for area relationships based on the simultaneous analysis of several taxa has become somewhat neglected (Parenti 2007). Donoghue and

Moore (2003) suggested that the search for area relationships was hindered by pseudo-congruence, which occurs when different area cladograms show the same area relationships, although the taxa diversified at different times, presumably under different underlying causes, and pseudo-incongruence, which occurs when area cladograms show conflict, but the taxa age indicates that they diversified in response to the same event. Different clades may have different temporal histories associated with different historical events, and the relative importance of each of these events can be segregated only if we estimate the timing of the origin/diversification of the

analyzed lineages (Cecca et al. 2011). Some authors have advocated molecular approaches, because they have the advantage of allowing estimation of the minimum disjunction age, thus avoiding inadequate comparisons. Unfortunately, most of these authors did not search for patterns based on different taxa and had assumed a great biogeographic complexity (Donoghue and Moore 2003; Sanmartín 2012; Batalha-Filho et al. 2013). The majority of the published phylogenetic analyses are still based on morphological data, especially for those taxa with rare species such as arthropods endemic to rain forests. This is the case of most harvestman taxa of the Brazilian Atlantic Forest, for which both time divergence estimations and fossil data are lacking.

The Atlantic Rain Forest of Brazil is one of the most threatened biogeographic areas in the world. Colonization by Europeans began there 500 years ago, and the majority of the most populous Brazilian cities are located within this region (Por 1992). It corresponds to the Atlantic biogeographical province of the Parana dominion (Morrone 2014a, 2014b). In the last few years, several phylogeographical studies of this area's species have been published (Pellegrino et al. 2005; Grazziotin et al. 2006; Carnaval et al. 2009; Fitzpatrick et al. 2009; Martins et al. 2009; Mata et al. 2009; Batalha-Filho et al. 2010; Thomé et al. 2010; D'Horta et al. 2011; Amaro et al. 2012; Amaral et al. 2013; Fusinato et al. 2013; Valdez and D'elía 2013; Cabanne et al. 2014; Dantas et al. 2015). Even though these studies have identified disjunctions within the forest biota, they were not intended to formulate explicit hypotheses on area relationships within the Atlantic Forest. The only analyses searching for area relationships were done by Amorim and Pires (1996) and Sigrist and Carvalho (2009). Silva et al. (2012) presented the main historical components using a track analysis.

Some studies have successfully used harvestman taxa to infer the evolution of biotas (Boyer et al. 2007; Hedin et al. 2012; Sharma and Giribet 2012), especially of the Atlantic Forest (Pinto-da-Rocha et al. 2005; Bragagnolo et al. 2015; DaSilva et al. 2015). The high endemism of harvestman taxa is considered an important feature that allows researchers to uncover unprecedented hypotheses of past disjunctions and events (DaSilva et al. 2015). Previous studies that showed area cladograms for the Atlantic Forest using harvestman phylogenies, however, were flawed in that they did not apply rigorous methodology, lacked some important areas of endemism or were published in book chapters with restricted circulation (Pinto-da-Rocha et al. 2005; DaSilva and Pinto-da-Rocha 2011; DaSilva et al. 2016). Therefore, a comprehensive and rigorous cladistic biogeographic analysis of harvestmen still needs to be done for the Atlantic Forest. This analysis should contribute to the understanding of the evolution of the Atlantic Forest and thus may be helpful for its conservation.

Our objective was to present a general pattern of historical relationships among areas of endemism in the Brazilian Atlantic Rain Forest based on the phylogenetic hypotheses of sympatric harvestman taxa, and contribute to unraveling its biotic evolution. We intend to empirically demonstrate that the search of biogeographic patterns puts forth a reasonable purpose.

Material and Methods

We used published species-level phylogenetic analyses of 6 subfamilies and a genus of Gonyleptidae (Opiliones) endemic to or characteristic of the Brazilian Atlantic forest (Table 1). *Promitobates* phylogeny is the only one based on molecular data and thus shows a time estimation for the divergence (Bragagnolo et al. 2015). The

authors did not include *P. weissbier* in this analysis, thus we assumed this species to be the sister to *P. viridigranulatus* based on an earlier morphological phylogeny (Bragagnolo and Pinto-da-Rocha 2012). Five of the nominal species of the genus resulted in a species complex (*P. ornatus* complex) with hybridization; thus, we treated them as a single terminal (Figure 1).

We used 12 areas of endemism (Figure 2) previously identified by DaSilva et al. (2015), in which the congruence of endemic harvestman species ranges were based, as terminals of the taxon-area cladograms. Each area of endemism contains a Congruence Core, defined by the distributional congruence criterion, and a Maximum Region of Endemism, given by the rest of the endemic species. The latter can be interpreted as transition zones between areas of endemism or imprecise hypotheses of congruence due to poor data sampling (DaSilva et al. 2015). Most species are endemic to one area, and only 3 out of the 130 species do not occur in any area of endemism. Taxon-area cladograms were constructed replacing each terminal species by the area(s) of endemism in which it occurred.

In order to find general area cladograms, we applied three different methods to construct area matrices according to taxa: 1) For primary Brooks Parsimony Analysis (BPA), we used all the information present in the taxon-area cladograms, coding all the nodes and terminals in the matrix (Wiley 1988; Brooks et al. 2001). It has been assumed that widespread taxa are "noise" when searching for phylogenetic congruence and historical signals, since the areas where they occur may have been colonized through recent dispersal events (Cracraft 1994; Nihei 2006); then 2) we also applied a variety of BPA in a second matrix shown in Figure 3, which only includes the information provided by the nodes and excludes the information from widespread terminal species in a second matrix (Kluge 1988); and 3) in a third matrix, we applied a paralogy-free (PF) subtree analysis shown in Figure 3, which is based on the information provided by the nodes without paralogy such as repetition of area relationships in the same lineage and redundant nodes (Nelson and Ladiges 1996). The nodes without paralogies (the subtrees) were chosen manually by examining all of the branches of the taxon-area cladograms from the tips to the root. The nodes with repeated areas were considered paralogues and excluded from the subtrees (Nelson and Ladiges 1996). This analysis was intended to exclude arbitrary area relationships such as those resulting from duplications, dispersals, or extinctions; this analysis might reflect more accurately historical area relationships (Nelson and Ladiges 1996).

We constructed 3 matrices (Figure 3): 1) primary BPA (BPA), 2) BPA with nodes (BPAn), and 3) PF subtrees. Matrices were constructed using areas of endemism as rows (the terminals of the analysis), and each column is a node (BPAn and PF) and a node or a terminal species (BPA) of the area cladogram of each taxon (the characters of the analysis). The state of each character is determined by the presence or absence (coded as 1 and 0, respectively) of each node or terminal species in the areas of endemism. For BPA and BPAn, areas of endemism absent in the taxon cladogram were coded as "?" (Wiley 1988). We ran the 3 matrices with a parsimony algorithm to find general area cladograms. Matrices were constructed using NDE version 0.5.0 (Page 2001). Parsimony analyses were carried out using TNT V.1.1 (Goloboff et al. 2000). The maximum number of trees saved to the programs' storage was set to 10,000, the number of replications was set to 1,000, and the swapping algorithm selected was TBR with 10 trees saved per replication.

We calculated the Incongruence Length Differences (ILD) between the general area cladograms that resulted from each partition of the entire matrix and sums of them (except when there was

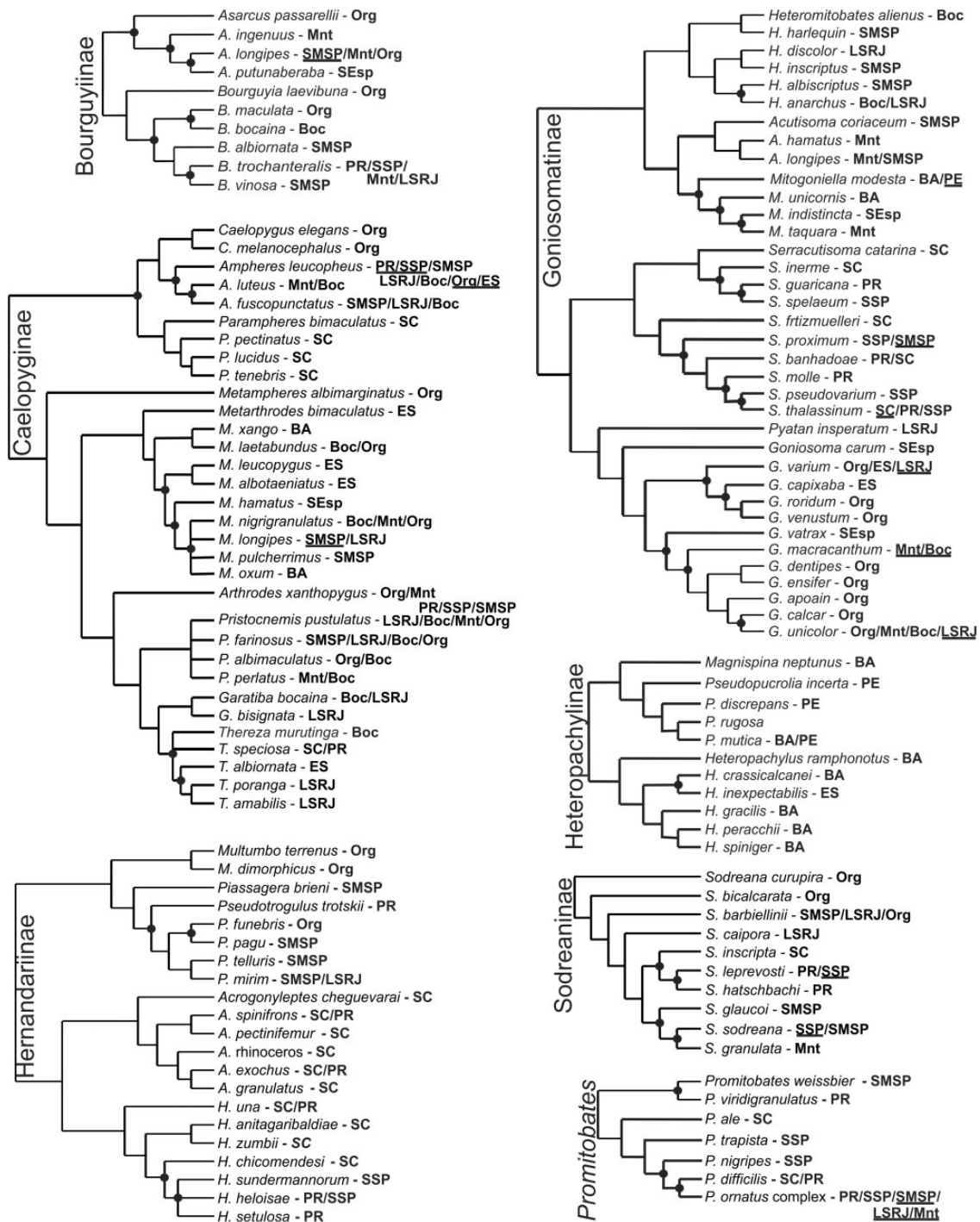


Figure 1. Taxon-area cladograms of the taxa analyzed. Black dots on nodes are the paralogy-free nodes and the underlined areas are included in the paralogy-free relationships.

overlap of characters between matrices; Figure 3) to evaluate the influence of each method and kind of information (such as nodes without paralogies and widespread species) in the results (Farris et al. 1995). A resampling test of significance of incongruence between matrices was done against a null model based on randomization of equally sized matrices (Farris et al. 1995). Thus, if there are different area relationships in different methods, we could expect a significant incongruence between the partitions. The ILD test was run in Winclada (Nixon 1999) with a function based on the “arn”

program, using commands “hold10; mult*30; hold/10” (Farris et al. 1995).

Results

BPA resulted in 2 general area cladograms ($L=232$, $CI=0.58$, $RI=0.6$), which differed in the relationship between the northern areas of endemism. BPA_n resulted in a single general area cladogram ($L=164$, $CI=0.57$, $RI=0.63$), similar to the consensus of both BPA

Table 1. Taxa analyzed, with the number of species of each taxon-area cladogram, the areas of endemism (see Figure 2) where they occur, the number of characters in the matrices of each method and the authors of the phylogenetic analysis

Taxa	Number of species	Areas of endemism	Number of characters in each matrix	References
Bourguyiinae	10	Boc, Mnt, Org, PR, SEsp, SMSP, and SSP	BPA = 11 BPAn = 9 PF = 6	Yamaguti and Pinto-da-Rocha (2009)
Caelopyginae	28	BA, Boc, ES, Mnt, LSRJ, Org, PR, SC, SEsp, SMSP, and SSP	BPA = 34 BPAn = 20 PF = 8	Mendes and Barros (2013); Mori and Pinto da Rocha (2014)
Goniosomatinae	36	BA, Boc, ES, LSRJ, Mnt, Org, PE, PR, SC, SEsp, SMSP, and SSP	BPA = 42 BPAn = 33 PF = 14	DaSilva and Gnaspini (2009)
Hernandariinae	21 (23) ^a	LSRJ, Org, PR, SC, SMSP, and SSP	BPA = 22 BPAn = 17 PF = 4	DaSilva and Pinto-da-Rocha (2010)
Heteropachylinae	10 (11) ^a	BA, ES, and PE	BPA = 7 BPAn = 7 PF = 1	Mendes (2011)
Sodreaninae	10	LSRJ, Mnt, Org, PR, SMSP, SC, and SSP	BPA = 11 BPAn = 9 PF = 4	Pinto-da-Rocha and Bragagnolo (2010)
<i>Promitobates</i> (Mitobatinae)	7 (11) ^b	LSRJ, Mnt, PR, SC, SMSP, and SSP	BPA = 8 BPAn = 6 PF = 3	Bragagnolo and Pinto-da-Rocha (2012); Bragagnolo et al. (2015)

Note: BPA, Brooks Parsimony analysis; BPAn, BPA of nodes; and PF, paralogy free subtrees analysis. ^a In parentheses, the total number of species of the taxon.

^b In parentheses, the number of nominal species—5 of them are considered a species complex by Bragagnolo et al. (2015) and are treated as a single terminal in the present analysis.

general area cladograms. PF resulted in 3 cladograms ($L = 79$, $CI = 0.5$, $RI = 0.59$), which overall showed different relationships, although some cladograms were similar to those of BPA and BPAn (Figure 4).

Two main groups of areas of endemism were found in all of the general area cladograms: a southern block (SSP, PR, and SC) and a southeastern block (Org, LSRJ, Boc, Mnt, and SMSP). A third group, consisting of the northern areas of endemism (PE and BA), was closely related to SEsp in BPA and BPAn cladograms and in 2 of the PF cladograms, whereas in the other PF cladogram PE was sister to all other areas of endemism (SEsp and BA are grouped together). ES varied more in its relationships, being sister to the southeastern block in BPA, BPAn, and one of PF general area cladograms, or more closely related to the southern block in 2 PF cladograms. The latter relationship was rather unexpected, since ES is geographically located more than 800 km away from the southern block, with the entire southeastern block being situated between them (Figure 2). All resulting general area cladograms can be represented in a general diagram showing the alternative relationships and polytomies (Figure 5). Dashed branches in Figure 5 show the alternative relationship of SEsp + BA, sister to southeastern and southern blocks, and PE sister of all the rest of areas. The 3 polytomies are a strict consensus of the 2 relationships of areas in the southern block, 2 relationships of areas in the southeastern block, and 2 relationships of ES to southern and southeastern blocks resulting from general cladograms (Figure 4). The ILD tests resulted in rejection of the hypothesis of incongruence between the partitions (Table 2).

Discussion

Methods and kind of phylogenetic information used to infer general patterns

The use of different methods and sources of information from the taxon-area cladograms allowed to find different general area

cladograms connecting the areas of endemism, which reflect the complex history of the Brazilian Atlantic Rain Forest. Some levels of reticulate histories of relationships among areas of endemism should be expected in terrestrial and continental biotas (Cracraft 1988; Brooks 1990; Andersson 1996; McLennan and Brooks 2002), because these entities have fuzzy limits, lacking sharp barriers between them or they have began losing their original delimitation (Cracraft 1988; Crisp et al. 1995; Roig-Juñent and Coscarón 2001). Furthermore, different organisms respond in different ways to the same historical event. Thus, even when major disjunctions are detected among large blocks of areas of endemism, dispersal events, and range expansions, extinctions and lack of speciation are common processes causing incongruence when comparing area cladograms of different taxa. In spite of this, a general pattern of relationship of Atlantic Forest areas of endemism could be inferred (Figure 5).

Three problems may cause noise when searching for general area cladograms: 1) widespread taxa; 2) missing areas; and 3) redundant distributions resulting from paralogy (Morrone 2009) as well as the obvious, poor taxon sampling. Using 3 different analytical methods, it was possible to observe the different biases caused by these problems. Grouping areas using the distribution of widespread taxa was done under BPA assumption 0 (Zandee and Roos 1987). Several authors have indicated the problem of using widespread taxa distributions to infer biogeographic relationships (Humphries and Parenti 1999; Brooks and Van Veller 2003; Ebach et al. 2005; Santos 2005). This information would only be correct if species were widespread due to non-divergence during the vicariance that resulted in areas of endemism (Brooks and Van Veller 2003; Santos 2005). Most of the widespread taxa, however, could occur because they recently colonized areas of endemism, thus reflecting ecological relationships rather than historical ones. In BPA, and even in BPAn, the

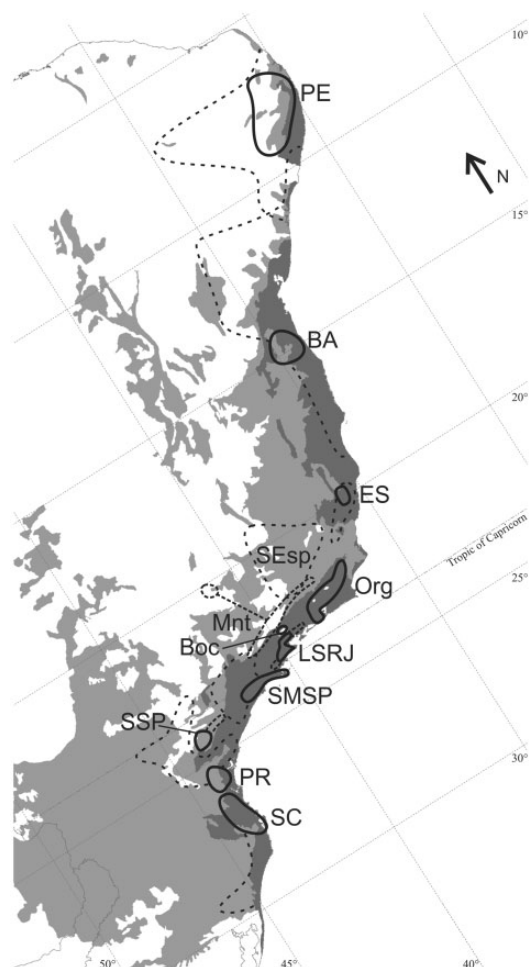


Figure 2. Areas of endemism for harvestmen of the Atlantic Rain Forest of Brazil used in the cladistic biogeographic analysis (modified from DaSilva et al. 2015). Full lines represent the Congruence Cores of the areas of endemism; dashed lines are the Maximum Regions of Endemism of the AoEs, which can be transition zones between 2 areas or regions with poor data sampling (see original discussion of DaSilva et al. 2015). Dark gray is the coastal forest (Dense Ombrophilous forests and adjacent Open Ombrophilous and marine influenced vegetation, according to IBGE 2004); light gray is the interior forest (other physiognomies of Atlantic Forest, IBGE 2004). BA, Bahia; Boc, Serra da Bocaina; ES, Espírito Santo; LSRJ, Southern Rio de Janeiro coast; Mnt, Serra da Mantiqueira; Org, Serra dos Órgãos; PE, Pernambuco; PR, Paraná; SC, Santa Catarina; SEsp, Serra do Espinhaço; SMSP, Serra do Mar of São Paulo; SSP, Southern São Paulo.

BPA (<i>n</i> =135; <i>L</i> =232)		
BPAn (<i>n</i> =100; <i>L</i> =164)		WS (<i>n</i> =35; <i>L</i> =59)
Pn (<i>n</i> =59; <i>L</i> =93)	PF (<i>n</i> =40; <i>L</i> =79)	WS (<i>n</i> =35; <i>L</i> =59)

Figure 3. Two partitions regimes (middle and bottom) of the entire matrix (BPA, top) used in ILDT tests representing different kind of information. BPAn, Brooks Parsimony Analysis of nodes; Pn, paralogous nodes; PF, paralogy-free subtree analysis; WS, only the information from widespread species distributions; *n*, number of characters of each matrix; *L*, length of resulted cladograms; in bold are the methods whose general area cladograms are inferred.

widespread information is still amplified because the character is replicated in more basal nodes progressing downward from widespread terminal taxa. Missing areas in most taxon hypotheses may result in their basal positioning in the general area cladograms. Redundant distributions in paralogous nodes are mostly repetitions of the same disjunction and increase incongruence for the same process. Nelson and Ladiges (1996) suggested that extracting the relevant information from the taxon-area cladograms would prevent the redundant information overflow the congruence inference (Ebach et al. 2005).

To deal with these 3 problems, we applied different methods to our data. When comparing the results of BPA, BPAn, and PF, we progressively reduced the importance of the widespread taxon information. It appears that grouping the northern areas of endemism (PE, BA, and SEsp) and ES with the southeastern block (Org, LSRJ, Boc, Mnt, and SMSP) was more influenced by widespread taxa, since the resulting PF presented alternative relationships. Regarding the second problem of missing areas, it is important to note that 3 out of the 7 taxa used in the present analysis occurred in the northern areas (Caelopyginae, Goniosomatinae, and Heteropachylinae) and the latter did not occur in the southern blocks. We used a “?” for matrix cells that are missing in each taxon-area cladogram in BPA and BPAn in order to reduce this problem (Wiley 1988; Andersson 1996; Brooks et al. 2001).

When addressing the third problem, only 40 out of 135 nodes used in BPA were considered PF in our data, and the resultant general area cladograms were different, even though some of the PF cladograms were similar to those resulting from BPA (Figure 4). Most of the paralogies can be related to duplications of area relationships such as SSP, PR, and SC in *Serracutisoma*; PE and BA in *Heteropachylinae*; and SMSP, Org, and Mnt in *Bourguiniinae* (Figure 1). These redundancies reveal a pattern of similar disjunctions in related taxa such as probable due to sympatric diversification or a secondary range contact of an early ancestor of these taxa. In addition to the differences between the general area cladograms resulting from different analyses, the ILDT test rejected the incongruence among the partitions (representing the methods and different kind of phylogenetic information). This may indicate that area relationships were maintained with few changes in widespread taxa, in PF nodes, and even in deeper-in-time paralogous nodes that are more common in basal placements of the cladograms (Figure 1). The above cited redundancy in area relationships is a pattern that partly explains the congruence of different cladograms.

It seems that the main barriers responsible for the diversification of harvestmen were effective at different times and were represented by different methods and the relative distance of informative nodes from the tips of the cladograms. The relationships of areas and the barriers that isolated them seem to have structured the ranges of widespread taxa in a recent ecological layer. Differences relating to more recent periods can be seen in the BPA results (Figure 4A), which indicate that close relationships between PE + BA, SC + PR, and LSRJ + Boc might have only been caused by widespread species. This suggests that the barriers between them were more effective in the past than in their current form or it may have had more recent biotic changes between those areas of endemism.

General patterns in the history of the Atlantic forest

Considering the biogeographical regionalization of Morrone (2014b), most of the areas of endemism analyzed are included in the Atlantic province except Mnt and SEsp, both of which belong to the Parana Forest province. The Atlantic province was divided by

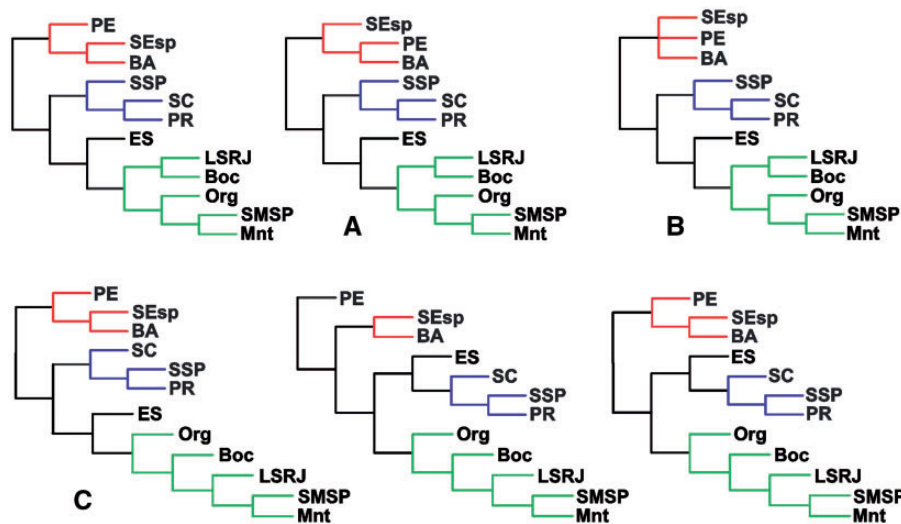


Figure 4. General area cladograms resulting from the three methods. (A) BPA (2 cladograms); (B) BPAn (1 cladogram); (C) PF (3 cladograms). Red is the northern block, green is the southeastern block, blue is the southern block.

Morrone (2014b) into 3 districts: 1) Pernambuco (herein PE); 2) Bahia (BA); and 3) Paulista (the southern and southeastern blocks). Details of a formal regionalization based on harvestman areas of endemism were given by DaSilva et al. (2015, Data S1).

The main geographical barriers associated with the general historical patterns (Figure 5) are the Valleys of the Doce, Paraíba do Sul, and Ribeira do Iguape Rivers and the Todos os Santos Bay. The importance of the Doce River and Todos os Santos Bay disjunctions are corroborated by many studies using different methods and taxa (Müller 1973; Prance 1982; Amorim and Pires 1996; Silva et al. 2004; Pellegrino et al. 2005; Sigrist and Carvalho 2009; Brunes et al. 2010; Thomé et al. 2010; Silva et al. 2012; Cabanne et al. 2014); the latter has also been associated with the São Francisco River (Carnaval and Moritz 2008). DaSilva et al. (2015) provided detailed geographical and historical information on the barriers between areas of endemism for harvestmen and also showed that the Todos os Santos Bay should receive more attention from biogeographers, because it is more closely associated with the range limits of endemic species (see also Amorim and Pires [1996] and Silva et al. [2012]). This is similar to the area around the Ribeira do Iguape River, where the barrier is related to its deep valley, but not to its water course (the area of endemism SSP is situated north of the river but is related to the southern block). Bragagnolo et al. (2015) estimated that the time of divergence of taxa separated by the Ribeira do Iguape River in the *Promitobates* phylogeny was ~50–56 million years ago (Mya). This agrees well with the estimate of the origin of the valley (Almeida and Carneiro 1998). Some analyses have shown the same barrier between the southeast and southern blocks but with different estimates of time divergence (~0.39–4.9 Mya) (Grazziotin et al. 2006; Batalha-Filho et al. 2010; Brunes et al. 2010; Silva et al. 2012; Cavarzere et al. 2014).

Some historical processes can be related to these barriers: 1) tectonism (the rivers and bay are important grabens and rift systems; Almeida and Carneiro 1998; Saenz et al. 2003; Saadi et al. 2005); 2) marine transgressions on the valleys (Martin et al. 1993; Suguio et al. 2005; Rossetti and Góes 2009); and 3) present-day xeromorphic or sandy-adapted vegetation mainly in the Paraíba do Sul Valley and north of Todos os Santos Bay (IBGE 1983; Joly et al. 1999; Figure 2). This can be related to forest reduction, resulting in

mesic refugia, during climatic fluctuations and global cooling since the Pliocene or late Miocene epochs (Holbourn et al. 2014; Ravelo et al. 2004).

An important issue related to the main difference between the northern areas of endemism (BA and PE), delimited by the barriers of the Doce River and Todos os Santos Bay, is the great difference in the climatic regime compared with the southern blocks (Carnaval et al. 2014). The former have more seasonal precipitation, because they do not receive the summer monsoon rains and seem to have had a different fluctuation system during the Pleistocene epoch with evidence of cold and humid periods (dipolar pattern of precipitation *sensu* Oliveira et al. 1999; Ledru et al. 2009; Cheng et al. 2013). Carnaval et al. (2014) used these differences to explain the phylogeographic endemism and diversification of the Atlantic Forest, considering that the areas of endemism of Bahia and Pernambuco had a more stable climate. This created larger refugia than the southern and southeastern areas of endemism, which suffered more drastic reductions in glacial periods. Another hypothesis to be tested is the role of climatic/latitudinal gradient in creating ecological speciation (Freedman et al. 2010) along the Atlantic Forest. Although we have indicated some processes that could be responsible for harvestman diversification in the area, the lack of a time estimation of most speciation events prevent us from rigorously testing this hypothesis. The estimated time divergence of the *Promitobates* species indicates that the last speciation event at ~5 Mya is older than Pleistocene refugia (Bragagnolo et al. 2015). Therefore, if forest reductions could have influenced those diversifications, ancient cooling in Miocene/Pliocene epochs could have caused this divergence (Ravelo et al. 2004; Holbourn et al. 2014).

It can be speculated that the general pattern found in this analysis can refer to the more humid portion of the Atlantic Forest, since endemic harvestmen are restricted to this ecosystem. The barriers presented herein should then have been greatly influenced by climatic fluctuations. In the southern and southeastern blocks, the polytomy in the general pattern (Figure 5) may indicate biotic changes between the areas of endemism, but with a clear endemic pattern in each one (DaSilva et al. 2015). This would be related to a refuge model of diversification, with dispersal events during humid periods and vicariance events during refuge periods. These refugia

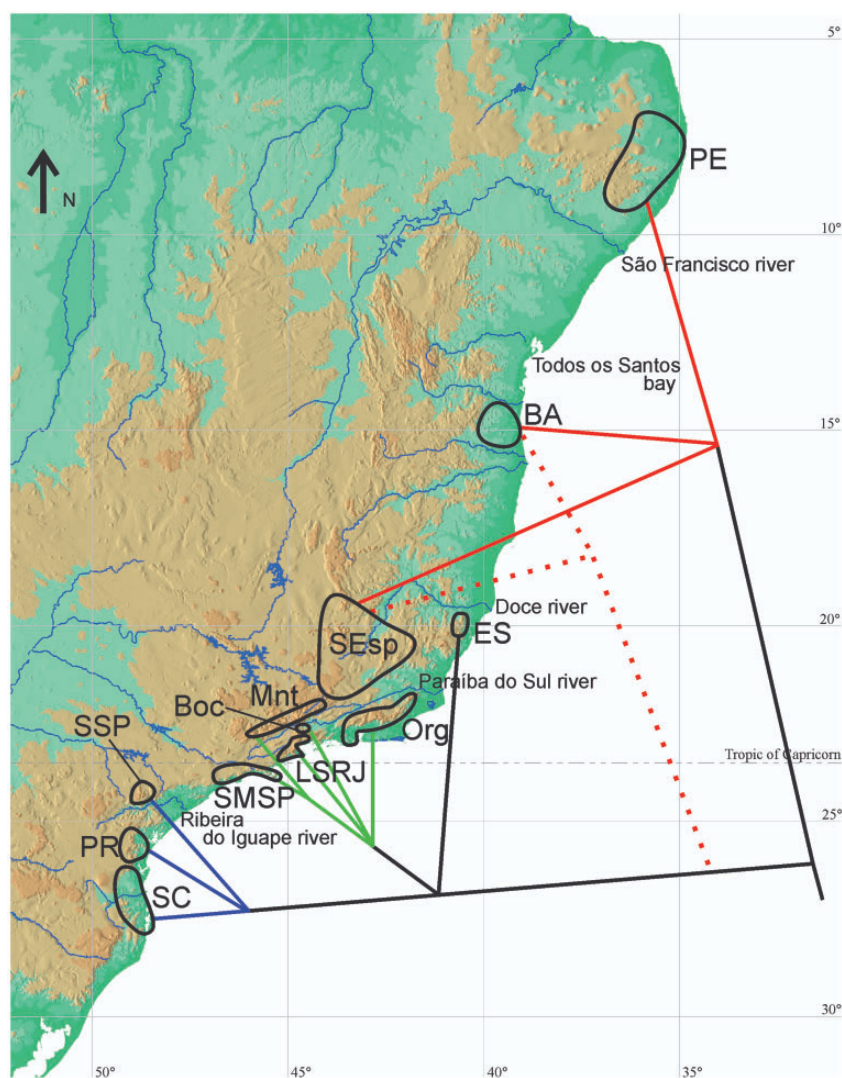


Figure 5. General pattern of relationship of areas representing all the resulting general cladograms on a topographic map. Red is the northern block, green is the southeastern block, blue is the southern block. Dashed branches represent an alternative relationship, that is, PE sister of all rest of the areas and SEsp and BA sister to southeastern and southern blocks (Figure 4). Polytomies are the strict consensus of alternative relationships of included areas (Figure 4).

Table 2. Results of Incongruence Length Difference tests of each partition pair of the entire matrix (Figure 3) representing the different methods and kind of information from taxon-area cladograms (partitions that overlap in the matrix were not calculated)

ILD test	Result
BPA _n × WS	No ($P = 0.9032$)
P _n × PF	No ($P = 0.5484$)
P _n × WS	No ($P = 0.9355$)
PF × WS	No ($P = 0.4194$)
P _n +WS × PF	No ($P = 0.5806$)

Notes: “No” means that incongruence was not significant (P). BPA_n, Brooks Parsimony Analysis of nodes; P_n, paralogous nodes; PF, paralogy-free subtree analysis; and WS, only the information from widespread species distributions.

would be more concentrated in the slope regions of mountain ranges, whereas the plains have been more subjected to reduction of forests (Haffer 1987; Por 1992; Carnaval et al. 2014; DaSilva et al. 2015). The lack of a clear relationship among the areas of endemism

in the southern and southeastern blocks, the redundancy in area relationships (mostly associated to paralogous nodes), and the congruence between results from methods with different phylogenetic information suggest that the diversification of harvestmen in the Atlantic Forest was driven by reiterative barriers (*sensu* Amorim [2009] and DaSilva et al. [2016]). This indicates that barriers working at multiple times in the same region resulted in a complex biogeographic pattern with a high spatial congruence in distributions of lineages and species. In the Atlantic Forest, the main barriers are valleys associated with important rift systems that have opened since the tectonic reactivation of the Paleocene (Saenz et al. 2003). These wide valleys have been more influenced by marine transgressions that covered them in the middle Miocene, early Pliocene, 3 times in the Pleistocene and 1 in the Holocene epochs, then are regions of high sedimentary deposition in humid periods and more erosion in arid periods (Hallam 1984; Domínguez et al. 1992; Martin et al. 1993; Suguio et al. 2005; Rossetti and Góes 2009). This led to high instability. Orographic rains, very common and partly responsible for the high humidity in most of the Atlantic Forest, were absent in

these regions, which would therefore prevent the development of humid forests. Since the Neogene period, these characteristics allowed for a greater reduction of the forests in these regions because of climatic fluctuations that would cause feedback to facilitate their instability. This model of diversification of reiterative barriers with spatial congruence at multiple times would respond to claims of individual taxa history when it is shown that different taxa diverge at different times in the same barrier (Brunes et al. 2010; Thomé et al. 2010; Cabanne et al. 2014). This represents an argument against pseudo-congruence (Donoghue and Moore 2003). In the case of the *Promitobates* time-estimated phylogeny, the barrier of the Ribeira do Iguape River seems to have separated 2 or 3 lineages at different times (~53 Mya for *P. ale* from the rest and ~22 Mya for *P. difficilis* from *P. ornatus* complex; Bragagnolo et al. 2015). This model still needs rigorous testing, using models of time of taxa divergence corresponding to divergences in geological events at the same locations.

In our study, we could find main disjunctions in humid portions of the Atlantic forest, which corroborated previous works with other approaches and taxa, namely the Doce, Paraíba do Sul and Ribeira do Iguape valleys, and the Todos os Santos bay. They have been interpreted as regions of long-term instability, which functioned as barriers at different times. Therefore, we hypothesize a model of diversification of reiterative barriers with spatial congruence at multiple times based on the general relationship of areas and its phylogenetic redundancy and the incongruence test of different partitions of the data.

Individual processes versus common patterns

Some authors have criticized some of the procedures that have been proposed to search for general congruence that imply aprioristic assumptions on the processes leading to incongruences (Brooks 1990; Brooks et al. 2001; Van Veller et al. 2002; Van Veller et al. 2003). These authors defend the idea that BPA can identify all the processes, including vicariance, dispersal, sympatric speciation, and vicariance without speciation. We may compare this search for congruence among taxon area-cladograms to phylogenetic systematics, where it is desirable to analyze adequate hypotheses about primary homologies. Thus, if we extract the appropriate information from the area-cladograms, and avoid paralogy or the influence of widespread taxa, we would achieve a better inference when searching for historical patterns of area-relationships (Ebach 2001; Ebach and Humphries 2002).

Even after dealing with these three problems and correcting for the noise in the data, our results still show some incongruence in the area relationships (Figure 4). Donoghue and Moore (2003) formalized some reasons for the lack of congruence reflecting the biotic history of a region; these reasons were named “pseudo-congruence and pseudo-incongruence”. A question is whether that biogeographical history is so complex that it cannot be inferred by cladistic biogeography. The individual phylogenetic/spatial histories of different taxa did have not enough distributional congruence to allow us to infer the history of an entire biota. In the present study we preferred to show a general pattern of disjunction (Figure 5) representing all the general cladograms found by different methods, but more importantly, also representing different temporal layers of disjunctions, rather than a single area cladogram. A dichotomic diagram would be a very simple representation for our aim, mainly in continental biotas, similar to those of the present study where there are no obvious barriers.

Early cladistic biogeography overestimated the power of inference of area cladograms, including the naïve reasoning that each node should be directly inferred as a vicariance event (Rosen 1978; Brooks et al. 2001). Currently, we have much more powerful methods to infer individual processes such as evolutionary models with molecular data or comparisons with potential distribution models (Graham et al. 2004). Platnick and Nelson (1978) postulated that unique distribution signals should unambiguously be inferred as dispersal events when there is a phylogeny with many nested nodes tipping to terminals living in a same area with a single apical terminal living in another area. Other distributional patterns need a model to infer probable biogeographic processes (Ronquist and Sanmartín 2011). It should be pointed out that cladistic biogeography searches for general patterns of disjunctions comparing phylogenetic hypotheses, an aim pursued by no other approach of evolutionary biogeography. This aim is still relevant (Parenti 2007) and contrasts with the argument that biogeographic complexity does not allow us to find common patterns and that each lineage has a unique history, totally independent of the history of the Earth (see very instructive discussions by Parenti and Ebach 2013a, 2013b and De Bruyn et al. 2013). This “unique-taxon-history” reasoning implies a complete dissociation of evolutionary and biogeographical thinking. Croizat’s (1962) dictum that “life and Earth evolve together” is still relevant for historical biogeography.

A renewal of cladistic biogeography and the search for patterns may be based on the following proposals: 1) to avoid considering only vicariance to explain common disjunctions, since patterns may be caused by dispersal and biotic changes in continental biotas; 2) to avoid indicating any processes to explain unique phylogenetic data or the need of searching for more evidence; 3) not to expect a single totally resolved general area cladogram for any region, because most of the areas are composite and biotic histories are reticulated; 4) to put a stronger emphasis in discriminating time-slices, if possible; 5) to end fragmentation in evolutionary biogeography; cladistic biogeography should interact with other approaches, including phylogeography; and 6) to highlight the biogeographic relevance and implications of each pattern found.

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