

A protocol for the delimitation of areas of endemism and the historical regionalization of the Brazilian Atlantic Rain Forest using harvestmen distribution data

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Abstract

The concept of areas of endemism (AoEs) has rarely been discussed in the literature, even though the use of methods to ascertain them has recently increased. We introduce a grid-based protocol for delimiting AoEs using alternative criteria for the recognition of AoEs that are empirically tested with harvestmen species distributions in the Atlantic Rain Forest. Our data, comprising 778 records of 123 species, were analysed using parsimony analysis of endemism and endemism analysis on four different grids (two cell sizes and two cell placements). Additionally, we employed six qualitative combined criteria for the delimitation of AoEs and applied them to the results of the numerical analyses in a new protocol to objectively delimit AoEs. Twelve AoEs (the most detailed delimitation of the Atlantic Rain Forest so far) were delimited, partially corroborating the main divisions previously established in the literature. The results obtained with the grid-based methods were contradictory and were plagued by artefacts, probably due to the existence of different endemism patterns in one cell or to a biogeographical barrier set obliquely to latitudinal and longitudinal axes, for example. Consequently, the congruence patterns found by them should not be considered alone; qualitative characteristics of species and clade distributions and abiotic factors should be evaluated together. Mountain slopes are the main regions of endemism, and large river valleys are the main divisions. Refuges, marine transgressions and tectonic activity seem to have played an important role in the evolution of the Atlantic Rain Forest.

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Introduction

The search for distributional patterns, areas of endemism (AoEs), and biogeographical classifications into regions or provinces are important aims that are integral to biogeography. AoEs represent hypotheses about the geographical units comprising (and defined by) endemic taxa (Crother and Murray, 2011) that have originated after the establishment of barriers that caused the isolation of the biota (Cracraft, 1985; Harold and Mooi, 1994; Linder, 2001; Morrone, 2001a). They are hypotheses based on spatial congru-

ence among restricted species ranges (Cracraft, 1985; Platnick, 1991; Morrone, 1994; Linder, 2001; Carine et al., 2009) and are the basic units of any historical biogeographical study (Cracraft, 1985; Morrone and Crisci, 1995; Crother and Murray, 2011). As hypotheses, AoEs can be refuted by new distributional data, by additional taxa or by historical reconstructions of the processes that determined the disjunctions that created them (Harold and Mooi, 1994; Morrone, 2001a).

Platnick (1991) and Morrone (1994) used the congruent distributional limits of two or more species as the main criterion for delimiting AoEs. However, real species ranges make it difficult to apply this criterion, as there is always incongruence in more detailed scales

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of observation (Cracraft, 1985). Delimiting AoEs is a complex task that involves the interpretation of partially overlapping species ranges and/or other kinds of evidence (e.g. Axelius, 1991; Harold and Mooi, 1994; Crother and Murray, 2011). Among the latter are sister-group relationships between species in adjacent AoEs or the geological/physiographical/ecological unity or limits of an area (Cracraft, 1985; Harold and Mooi, 1994; Riddle, 1998).

Many methods have been proposed and programs have been written to delimit AoEs, but they have been poorly used with real data, except for parsimony analysis of endemism – PAE (e.g. Hausdorf and Hennig, 2003; Szumik and Goloboff, 2004; dos Santos et al., 2008). Some authors have criticized the use of areas and analyses of endemism in historical biogeography and have proposed alternative approaches as methods to search for barriers (e.g. Arias et al., 2011). Indeed, despite the great importance of AoEs in historical biogeography, their definition and the criteria to delimit them have not been sufficiently discussed in the literature (Crother and Murray, 2011).

The Atlantic Rain Forest of Brazil, even when compared with the Amazon Forest, is a mega-diverse biome. Furthermore, more than 50% of the plant and animal species in the former (Mittermeier et al., 2005), including 97.5% of the harvestmen species (Pinto-da-Rocha et al., 2005), are endemic. The Atlantic Forest, recognized as one of 34 hotspots for conservation, is also one of the most endangered biomes in the world (Mittermeier et al., 2005). Despite the importance of this biome, few studies have focused on its biogeographical history. Exceptions include some phylogeographical accounts (e.g. Grazziotin et al., 2006; Martins et al., 2009; Thomé et al., 2010) and studies aiming to ascertain provinces and AoEs, some of which do not discriminate them from purely ecological divisions (e.g. Silva and Casteleti, 2005).

The Atlantic Forest is currently divided into two to six AoEs, depending on the taxa used to delimit them (Müller, 1973; Prance, 1982; Cracraft, 1985; Soderstrom et al., 1988; Amorim and Pires, 1996; Costa et al., 2000; BirdLife International, 2003; Silva et al., 2004; see Supporting Information Table S1). Those studies suffer from a few problems; for instance, they are insufficiently explained and sometimes use an inappropriate methodology (e.g. using only one size of grid-cells or manual delimitation). However, they have all employed the basic concept of congruence of restricted species ranges to delimit their AoEs.

Most studies in the Atlantic Forest have delimited three AoEs: one with its core in the state of Pernambuco, a second with its core in the southern portion of the state of Bahia and a third associated with the Serra do Mar mountain range (Table S1). However, even when the biogeographical divisions of the biome in

AoEs are congruent, the boundaries of AoEs may be quite different.

The endemism patterns of the Atlantic Forest harvestmen species are more restricted than those of other organisms (Pinto-da-Rocha, 2002; Pinto-da-Rocha et al., 2005; DaSilva and Pinto-da-Rocha, 2011). This high level of endemism is a function of some biological characteristics of the group, such as low vagility and high hygrophily (Pinto-da-Rocha et al., 2005). Pinto-da-Rocha et al. (2005) delimited 11 AoEs based only on the congruence of at least three endemic species. However, their study lacks a detailed description of the methodology they used.

In this contribution, we propose a protocol for the delimitation of AoEs using the distributions of harvestmen species in the Atlantic Forest as a model. Our protocol employs qualitative combined criteria to analyse data obtained by grid-based methods; therefore, it contributes to the discussion of AoE concepts.

Material and methods

Species and records

We analysed 773 records of 123 harvestman species of the suborder Laniatores, which are endemic to the Atlantic Rain Forest and belong to the following recently reviewed taxonomic groups: gonyleptids in the subfamilies Caelopyginae (Pinto-da-Rocha, 2002), Goniosomatinae (DaSilva and Gnaspini, 2009), Heteropachylinae (Mendes, 2011), Bourguiiinae (Yamaguti and Pinto-da-Rocha, 2009), Hernandariinae (DaSilva and Pinto-da-Rocha, 2010), Progonyleptoidellinae (Kury, 2003) and Sodreaninae (Pinto-da-Rocha and Bragagnolo, 2011); Stygnidae genus *Pickeliana* (Hara and Pinto-da-Rocha, 2008); Escadabiidae; Zalmoxidae; and Kimulidae (see species list in Supporting Information, Table S2). A. P. González and A. B. Kury (pers. commun.) studied the harvestmen of the last three named families. Taxa represented by a single record (19 spp.) were not included in the analysis. Two species were excluded because they do not overlap with any other species (Fig. 1).

Localities were compiled and reviewed from three sources: literature data; labels from specimens deposited at the Museu de Zoologia (Universidade de São Paulo), Museu Nacional (Universidade Federal do Rio de Janeiro) and Instituto Butantan; and collecting data obtained by the authors in 41 localities.

Numerical methods

Two numerical methods were employed using a map divided into cells. In PAE, the cells on the map were treated as terminals (Morrone, 1994), and Nona 2.0 was used to analyse the data (Goloboff, 1999). To perform

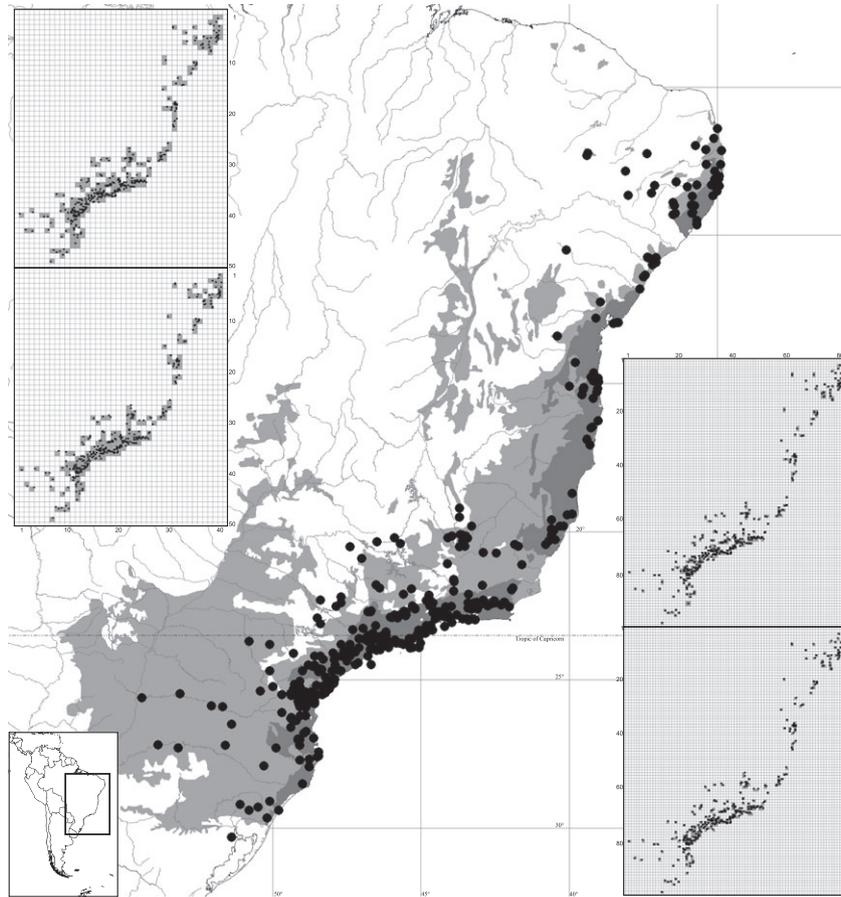


Fig. 1. All records and four grids used in the analyses: above left, 0.5° -cell grids; below right, 0.25° -cell grids, up and down $0'$ -origin and $12'$ -origin grids, respectively, with cell numbers. Dark shading indicates moist coastal forest; light shading indicates interior forest.

the endemism analysis, a method described by Szumik and Goloboff (2004), we used NDM/VNDM (Goloboff, 2005). Cell sizes were set to 0.5° and 0.25° (both methods), and each was specified with two different origins to form grids ranging from 6° to $30^\circ 30'S$ and from $34^\circ 30'$ to $55^\circ 30'W$ (both methods), and from $6^\circ 12'$ to $30^\circ 42'S$ and from $34^\circ 42'$ to $55^\circ 42'W$ (only NDM; Fig. 1). These grids will subsequently be referred to as $0'$ -origin and $12'$ -origin grids, respectively.

In NDM, we used the default factor $F = 0.5$, which means that an occurrence outside the area, or a lack of records inside that, is worth half of an occurrence in the cell in the area; preliminary runs with other values of F gave us similar results (data not shown). To use only the raw data and to make as few assumptions as possible about the distributions of species, we turned off 'assumed presences' or 'edge proportion' (Goloboff, 2005). Furthermore, records obtained on the borders of cells were used in only one cell per matrix to avoid duplication of records. In such cases, we employed the following criteria to assign a record to a given cell: first, we gave preference to the cell that had records of other species, or to the cell that was closest to the next nearest record of the species; if nei-

ther one of those two criteria was met, we chose the cell with more records of other species.

Qualitative analyses

We also employed six qualitative criteria to evaluate patterns of endemism for harvestmen (Box 1; Fig. 2). They were compiled from the literature or are proposed herein based on our data.

Protocol for delimitation of AoEs (four steps)—relating numerical methods to the qualitative combined criteria:

Step 1: For delimitations using grid-based numerical methods, different grid sizes and placements (origins in NDM) should be tested (Morrone and Escalante, 2002; Deo and DeSalle, 2006).

Step 2: In the NDM analysis, use consensus options. We used a strict consensus or tight consensus rule (Szumik et al., 2006; Aagesen et al., 2013) with a minimum number of shared species, i.e. different sets of cells containing at least one species in common were clustered (we used at least 5% of similarity in species). This is conceptually based on

Box 1

Qualitative combined criteria for delimitation of AoEs, with their corresponding literature references (Fig. 2).

(C1) Congruence of at least two species ranges (Platnick, 1991; Morrone, 1994; Linder, 2001; Carine et al., 2009). Referred to as ‘Congruence Core’ (CC, proposed here), this criterion is based on a considerable overlap of two species ranges. Complete overlap is not necessary as it is uncommon in distributional data. This sympatry is found by numerical methods such as PAE or NDM.

(C2) ‘Maximum Region of Endemism’ (MREs, proposed here). Species ranges often overlap only partially with the CCs. Partially overlapping species ranges may be due to the following: (1) widespread species (recorded in two or more cores), and (2) species that occur in only one core and outside of it but never inside the limits of another AoE core. In the latter case, species tend to have broader ranges than species restricted to a single core. Thus, the MRE is delimited around the CC with the extra range of every species that occurs only in this AoE.

(C3) General congruence of widespread species ranges is not a criterion for the delimitation of AoEs; only congruence of small ranges is evidence of an AoE (Deo and DeSalle, 2006). Deo and DeSalle (2006) proposed indices to distinguish endemism patterns from broader congruence patterns. Qualitatively, we can find widespread species, as defined above, when they occur in more than one CC. Thus, in a given scale of analysis, the congruence of widespread species (i.e. including two or more smaller AoEs) should not be defined as an AoE.

(C4) AoEs must be mutually exclusive (Linder, 2001; Crother and Murray, 2011). Because they are hypotheses concerning the isolated evolution of a biota, AoEs cannot be delimited in a contradictory way. That is, two AoEs cannot overlap or be identifiable by the same endemic species (Moline and Linder, 2006; Carine et al., 2009).

(C5) AoEs can be recognized even when there is not enough congruence among species ranges, but endemic species (outside any CC) are distributed near one another. Consequently, some species might not occur in any CC but present some degree of overlap among themselves. If those species have their sister species in adjacent AoEs, they can be used as another piece of evidence for the delimitation of AoEs.

(C6) Independent geographical evidence (Harold and Mooi, 1994; Riddle, 1998; Crother and Murray, 2011). As a hypothesis of historical unity, we can use evidence other than species distributions such as topographic or physiognomic data. For example, species endemic to the same topographical feature can delimit an AoE even if they do not overlap.

criterion C5 cited in Box 1, which states that AoEs must be mutually exclusive.

Step 3: Begin area delimitation using the results of the grid with smaller cells that represent the CCs of areas. Then, we delimited from more detailed to less detailed grids. The grid with larger cells results in the following: (1) areas not found when using smaller cells, (2) sums of or contradictions with the sets of smaller cells (see criterion C3) or (3) artefacts caused by one cell covering different AoEs (see Discussion). Next, delimit new areas with larger cells in the first case (1) and consider the results of smaller cells in two latter cases (2 and 3).

Step 4: Once the results of the numerical analyses delimit the CCs of AoEs (Box 1), the next step is to classify all species analysed into one of the following levels of endemism (criterion C2): (1) species restricted to CCs, indicated by numerical methods; (2) species that occur only in one CC but whose distributions are not sufficiently congruent (and therefore not detected by numerical methods), forming an MRE; and (3) species distributed in more than one

CC (i.e. widespread). Species that do not occur in any CC should be removed from the analyses if not overlapping with any other, or a new AoE can be delimited if there are two or more range-restricted species living in the same geographical unity (criteria C5 and C6).

Results

Results of the numerical analyses

The consensus trees obtained with PAE resulted in the following: (1) with the 0.5°-sized cells, nine sets of cells with two or more unique species (Fig. 3a; Table S3, Fig. S1); (2) with the 0.25°-sized cells, only three sets with more than one exclusive species (Fig. 3b; Fig. S1). Both analyses resulted in one set nested within another larger set: ((a23–33, a24–33)a21–34) (Fig. 3a; sets 3–4) and (a50–67, a49–67(a48–67, a47–67)) (Fig. 3b; set 11).

NDM/VNDM resulted in 11 and nine consensus-sets (from 23 and 17 original sets) using 0.5°-sized cells

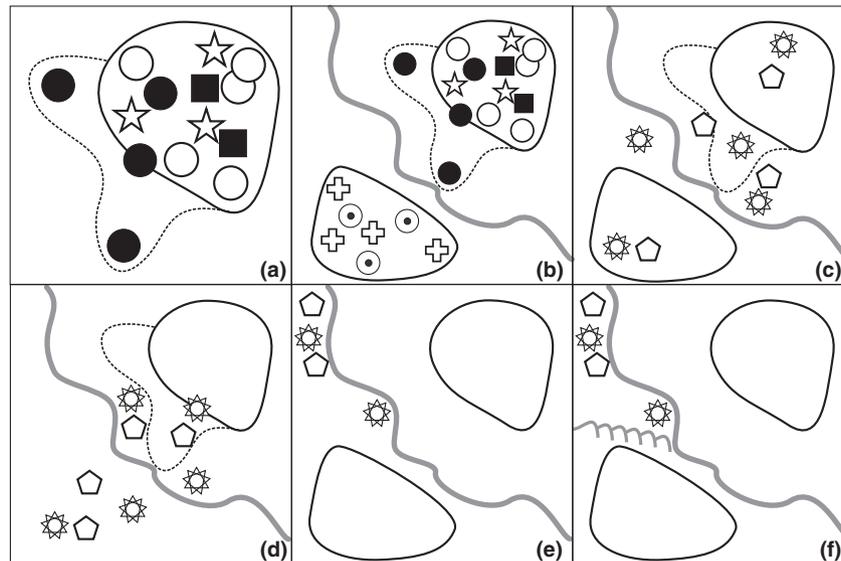


Fig. 2. Hypothetical examples of the use of qualitative combined criteria. (a) Criterion C1 allows the delimitation of a Congruence Core (CC, solid line) based on three species (white circle, white star and black square). (b) Criterion C2 allows the delimitation of a Maximum Region of Endemism (dashed line) based on a species occurring in a CC but not occurring in any other (black circle). (c) Criterion C3 would avoid a delimitation of an AoE by congruence range of widespread species (white sun and white pentagon). (d) Criterion C4 would avoid overlapping CCs, as they must be mutually exclusive (one of them could be delimited by white sun and white pentagon species). (e) Criterion C5 indicates that two endemic species (white sun and white pentagon) may be evidence of another AoE, even with poor range congruence. (f) Criterion C6 corroborates this new AoE shown in (e), because it is on the other side of a large river and a mountain range (grey lines) of the same topographical unit.

(Fig. 3c,d) and eight and seven consensus-sets using 0.25° -sized cells (from 11 and 12 original sets; Fig. 3e,f) for both grid origins. Some consensus-sets overlapped with each other; they more often overlapped with the analyses of 0.5° -sized cells (Fig. 3c, sets 15–19 and 22 overlap 21 and 23 in the $0'$ -origin grid; and Fig. 3d, sets 26–30 and 31–32 in the $12'$ -origin grid). Analyses using 0.25° -sized cells resulted in one pair of overlapping consensus sets (Fig. 3e; sets 34 and 35) and an overlapping of three sets (Fig. 3e; sets 34, 36 and 37), both with a $0'$ -origin grid. With the $12'$ -origin grid, we recovered one overlapping set (Fig. 3f; set 43 with 42 and 44). All other consensus sets were disjunct and thus can be considered putative AoEs.

Combining and interpreting the results

Following the protocol described above, we checked the results observing more detailed grid analyses (0.25°). We then delimited six putative CCs based on the analysis of the 0.25° -sized cell grids with a $12'$ -origin grid, the results of the consensus from the NDM analysis (Fig. 3f; sets 41–42 and 45–48). We also delimited the set 44 with a single cell, which was found manually, as NDM only finds sets with two or more cells. Sets from the $0'$ -origin grid are similar but overlap more (i.e. more cells are included in different sets). Based on criterion C5, we considered only scenarios with disjunct sets, as presented in the former analysis. For disputed sets, we considered the smaller set, as

indicated by criterion C3 (e.g. set 44 and 45 is preferred to set 36, Fig. 3e,f). Three sets found with PAE were congruent with three sets found with NDM (Fig. 3b; sets 10–12).

We then searched the less detailed grid (0.5°) for sets that were different from those already indicated above. In the $0'$ -origin grid analysis, we delimited two new CCs in NDM (Fig. 3c; 13 and 20); one of them was also found by PAE (Fig. 3a; set 7). In the $12'$ -origin grid analysis, we found an additional set (Fig. 3d; set 25), and PAE found the same set (Fig. 3a; set 1). The other set found in the $12'$ -origin grid analysis is similar to one of the $0'$ -origin grid analysis (Fig. 3c,d; set 24 = 13). PAE found one set with a single cell that was not found by NDM (Fig. 3a; set 4) because NDM only finds sets with two or more cells.

Thus, all the numerical analyses combined recover ten AoEs for harvestmen in the Atlantic Rain Forest (Fig. 4; Table 1) based on the CCs delimited by range congruence.

Following step 4 of the protocol above, we classified all species as restricted to ten CCs, discriminating MREs based on species occurring in only one core but not restricted to it (Table 1), and species not included in cases above.

In summary, ten AoEs are based on the following sets (Fig. 3; north–south): (area 1) 13 = 24; (2) 1 = 25; (3) 2 = 10 = 14 = 33 = 41; (4) 3 + 5 = 11 = 15 = 26 = 35 = 42; (5) 4 = 44; (6) 37 = 45; (7) 6 = 12 = 19 = 30 = 38 = 46; (8) 7 = 20; (9) 8 = 21 = 31 = 39 = 47; (10) 9 = 23 = 32 = 40 = 48.

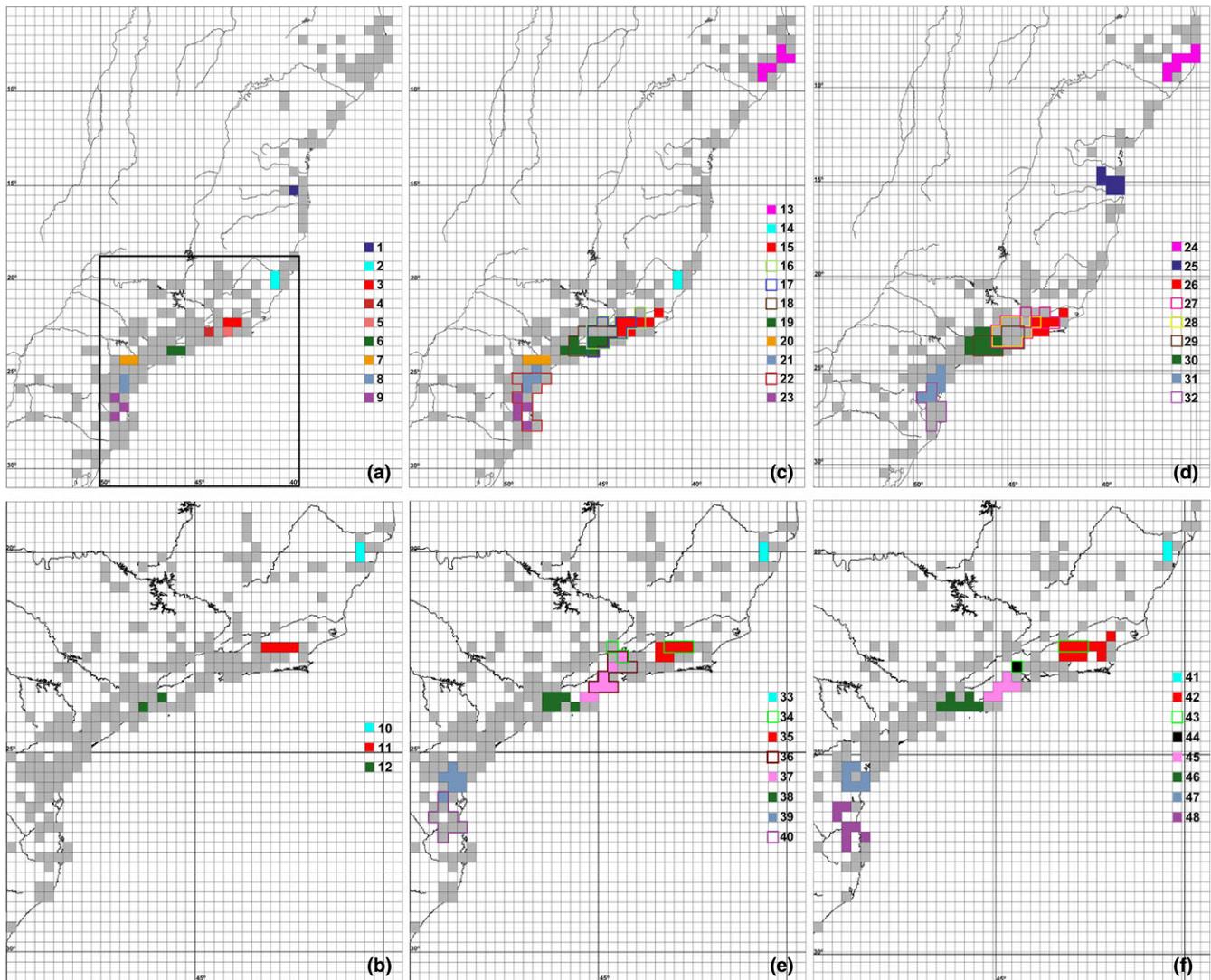


Fig. 3. Results of numerical analyses on a map. (a, b) Cell-sets are the consensus of parsimony analysis of endemism with (a) 0.5° and (b) 0.25° cell-grids. (c–f) Cell-sets are the consensus of NDM with (c, d) 0.5° and (e, f) 0.25° cell-grids and (b, e) 0'-origin and (c, f) 12'-origin grid. In each map, the legend shows the numbers of sets. Box in A is the area shown in b, e and f.

We follow the names of the AoEs proposed by Pinto-da-Rocha et al. (2005) and DaSilva and Pinto-da-Rocha (2011); see Table 1 and Fig. 4. Lastly, we present two other putative AoEs that were not found in the present numerical analyses but which can be individualized qualitatively (Fig. 4).

AoEs of the Atlantic Rain Forest based on harvestmen species ranges

The AoEs proposed here are delimited on the map in Fig. 4, and their corroboration using numerical methods is also presented (details of delimitation in Supporting Information, Tables S2 and S3). They are formally described based on the International Code of Area Nomenclature (Ebach et al., 2008) in Supporting Information Data S1. Acronyms follow Pinto-da-Rocha et al.

(2005) and DaSilva and Pinto-da-Rocha (2011): (1) Pernambuco (PE), (2) Bahia (BA), (3) Espírito Santo (ES), (4) Serra dos Órgãos (Org), (5) Serra da Bocaina (Boc), (6) Southern Rio de Janeiro coast (LSRJ) (7) Serra do Mar of São Paulo (SMSP), (8) Southern São Paulo (SSP), (9) Paraná (PR) and (10) Santa Catarina (SC).

Two putative AoEs that are based on criteria C5 and C6 were not found in our numerical analyses.

Serra da Mantiqueira (Mnt). Four species were not recorded in any of the above delimited AoEs, but they are restricted to the southern portion of the Serra da Mantiqueira mountain range and overlap slightly with the Itatiaia National Park (Pinto-da-Rocha et al., 2005).

Serra do Espinhaço (SEsp). This proposed AoE is the only one that is completely covered by the Montane

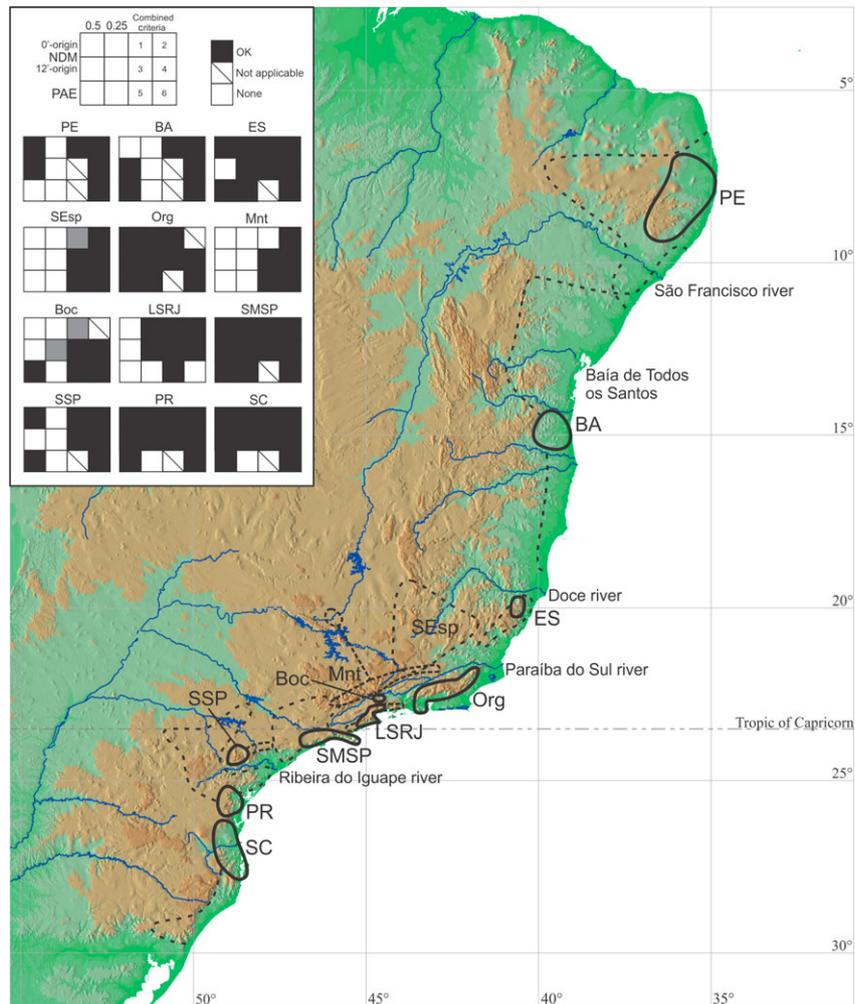


Fig. 4. Delimitation of AoEs on a topographical map of the Atlantic Forest. Full lines are the Congruence Core of AoEs, and dashed lines are Maximum Region of Endemism of AoEs. Main geographical locations of barriers are indicated. Inset: diagram (Navajo rug) showing results of analyses for each AoE. In each one, the four above left boxes are NDM results, two below left boxes are PAE results, and six boxes to the right are qualitative combined criteria. Grey boxes in SEsp indicate that there is some congruence range among endemic species despite an AoE not being found in numerical analyses; in Boc they indicate that congruence is based on a single locality, and it was only found manually in NDM with 12'-origin and 0.25°-cell grid. PE = Pernambuco, BA = Bahia, ES = Espírito Santo, SEsp = Serra do Espinhaço, Mnt = Serra da Mantiqueira, Org = Serra dos Orgãos, Boc = Serra da Bocaina, LSRJ = Southern Rio de Janeiro coast, SMSP = Serra do Mar of São Paulo, SSP = Southern São Paulo, PR = Paraná and SC = Santa Catarina.

Semi-deciduous Seasonal Forest included in the Province Parana Forest (Morrone, 2001b; Pinto-da-Rocha et al., 2005). The species that determine this AoE delimitation overlap very little in their ranges but are endemic in the same geographical unit (southern slopes of Serra do Espinhaço), distributed close to each other, and very distant from any other AoE.

Discussion

Grids, numerical methods and qualitative combined criteria

Delimiting AoEs using numerical methods has many problems, related largely to the use of grids as well as biases inherent to the methods. Our results show that

a less detailed grid with larger cells results in more AoEs than a grid with smaller cells (as in Morrone and Escalante, 2002). Also, larger cells can include two AoEs as well as important barriers between them or limits between pairs of allopatric species (Moline and Linder, 2006). When the placement of the grid is changed, these problems are transferred to other geographical points. The effects of cell size and placement in the present results can be visualized in the sensitivity boxes of Fig. 4. The use of different grids in this type of analysis yields more complete results (Morrone and Escalante, 2002; Deo and DeSalle, 2006; Casagrande et al., 2009a) as also stated in our protocol.

Different numerical analyses seem to give biased results (e.g. Moline and Linder, 2006; Carine et al.,

Table 1

The number of harvestman species restricted to Congruence Core (CC), Maximum Region of Endemism (MRE) and widespread, cell-sets resulting from numerical analyses as shown in Fig. 3, and number of published studies mentioning each AoE

AoE	CC	MRE	Endemic	Widespread	Literature citations	Sets of numerical analyses (Fig. 4)
PE	7	4	11	0	7	13, 24
BA	3	7	10	0	4	1, 25
ES	2	2	4	1	1	2, 10, 14, 33, 41
SEsp	0	6	6	3	0	–
Mnt	0	4	4	11	0	–
Org	14	0	14	11	*	3, 5, 11, 15, 26, 34, 42
Boc	3	0	3	11	*	4, 44
LSRJ	2	2	4	12	4	37, 45
SMSP	11	4	15	12	*	6, 12, 19, 30, 38, 46
SSP	2	1	3	8	*	7, 20
PR	4	5	9	11	*	8, 21, 31, 39, 47
SC	4	5	9	5	*	9, 23, 32, 40, 48
Total	52	40	92	31		

PE = Pernambuco, BA = Bahia, ES = Espírito Santo, SEsp = Serra do Espinhaço, Mnt = Serra da Mantiqueira, Org = Serra dos Orgãos, Boc = Serra da Bocaina, LSRJ = Southern Rio de Janeiro coast, SMSP = Serra do Mar of São Paulo, SSP = Southern São Paulo, PR = Paraná and SC = Santa Catarina.

*These AoEs are cited in four studies as a single AE.

2009) and neglect certain characteristics of a given AoE (e.g. Harold and Mooi, 1994; Crother and Murray, 2011). Thus, we listed six criteria to obtain the most likely AoEs as the smallest natural, spatial–historical hypotheses of biotic isolation. Delimiting CCs and MREs as well as classifying species ranges into three levels of endemism (criterion C2) allows the correct definition of the limits of AoEs and the resolution of partial sympatry patterns; this raises questions about the identity and limits of AoEs defined only by congruence (Hausdorf, 2002; Carine et al., 2009). Thus, by using criterion C2, the delimitation hypothesis gives explanatory power for all species analysed (not just the endemic and congruent species), something a numerical method cannot do.

MREs can be interpreted as hypotheses of events, such as dispersal or biological expansions after isolation (ontological interpretation) or as an indication that AoE delimitations can be falsified (methodological interpretation), mainly, when MREs resulted from insufficient data. Such regions have an important implication to do with the gradient of environmental changes between AoEs or transition zones (e.g. *Pernambuco–Bahia* or from some AoEs to the interior of the continent). A criticism of the AoE framework of common range patterns is that congruence in species ranges can be a result of collecting biases (e.g. more heavily sampled locations would tend to correspond to the core of AoEs). Comparing our data with those of Pinto-da-Rocha et al. (2005), we found that of the 26 well-sampled locations of the Atlantic Rain Forest, eight are very species-rich and are delimited as MREs in the present study. They probably comprise species from different historical origins (or a transition between AoEs).

Regional differences in the sampling effort, easily illustrated based on the density of points on the map, could influence the results of AoEs (Casagrande et al., 2009b). A well-sampled region would tend to result in more AoEs, as very sparse species records would not be sensitive to numerical analyses (Casagrande et al., 2009b). Ferrari et al. (2010), for example, showed that no area was delimited in poorly sampled regions of their data, which was different from our findings. On the other hand, critics might argue that a well-sampled region with uniformly distributed points could complete a pattern of gradual substitution, for example, resulting in fewer areas. It could further demonstrate that AoEs are artefacts of well-sampled regions separated by poorly sampled ones, as discussed in the paragraph above. This problem was minimized here by using grids of different cell size that resulted in different areas in each treatment: larger cells found areas in the poorly sampled north-east (*Pernambuco* and *Bahia*), and small cells were more sensitive to the well-sampled south-east region (other areas). We are confident about the likelihood of these patterns, as most harvestmen species have wider ranges in the north-east. More specific empirical studies are needed to address this important issue.

It is a common result of NDM to find sets that include two or more AoEs encompassing one large area, as in our results (Moline and Linder, 2006; Carine et al., 2009; Casagrande et al., 2012; Aagesen et al., 2013). In such cases, it is important to use the consensus option (step 2 of the protocol) in NDM (Aagesen et al., 2013). Furthermore, criterion C4 states that two AoEs cannot overlap or be nested within a top hierarchy at a given scale of the analysis, as AoEs are the result of geographical isolation. Thus, steps 3

and 4 of our protocol indicate how AoEs can be objectively chosen among results with a large number of overlapping and nested cell-sets. A hierarchy of levels of endemism has to be treated as a hypothesis of relationships of AoEs (Porzecanski and Cracraft, 2005) and can be used in the regionalization of provinces, regions and realms (e.g. Morrone, 2001b). Thus, such ‘wide congruence’ can result from many biogeographical phenomena such as dispersal after isolation or lack of response to isolating events.

The criteria of exclusivity of patterns (C4 and C5) and independent geographical evidence (C6) were applied to delimit the putative AoEs *Serra da Mantiqueira* and *Serra do Espinhaço* (and, to some degree, *Serra da Bocaina*), which had not been found by any numerical analyses.

In conclusion, results obtained with numerical methods should not be directly interpreted as AoEs. Because they are simply a guide for further analysis using objective criteria such as qualitative combined criteria based on the various concepts of AoEs, the units found with numerical methods such as NDM should be fine-tuned by eliminating overlapping and unstable sets as well as noise.

Areas of endemism in the Atlantic Rain Forest

Of the 12 AoEs delimited here, only two held for other groups of organisms with similar boundaries: *Pernambuco* and *Bahia* (Table 1). *Espírito Santo* was found in only one other publication (NRJ of Amorim and Pires, 1996). The other nine were ‘subdivisions’ of the large south-eastern area of the Atlantic Rain Forest that were considered to be a single AoE by several previous studies (e.g. *Serra do Mar*; Table 1) (see below).

Some characteristics of harvestmen biology in the Atlantic Rain Forest may have contributed to them reaching their present degree of isolation and diversification, such as hygrophily (due to a propensity for rapid dehydration) and low vagility (Santos, 2007). These characteristics restrict most harvestmen to very humid habitats, which are generally found in more mature and less anthropically disturbed forests (Bragagnolo et al., 2007). Some researchers have shown that harvestmen in the Atlantic Rain Forest are highly philopatric (Machado et al., 2000; Mestre and Pinto-da-Rocha, 2004; Willemart and Gnaspini, 2004). Thus, anything separating forested areas such as tectonic events, rivers, glaciation or open vegetation can split harvestmen populations.

Main events that created AoEs

We identified three kinds of possible barriers between AoEs (Fig. 4): large rivers reaching the Atlan-

tic Ocean such as the São Francisco (*Pernambuco–Bahia*), Doce (*Bahia–Espírito Santo*), Paraíba do Sul (*Espírito Santo–Serra dos Órgãos*; *Serra da Bocaina–Serra da Mantiqueira*, *Serra dos Órgãos–Serra do Espinhaço*) and Ribeira do Iguape (*Paraná–Southern São Paulo*); the tops of mountain ranges (*Southern Rio de Janeiro coast–Serra da Bocaina*); and disruptions in the physiognomy of the forest as found around the Paraíba do Sul River where there is xeromorphic vegetation (Joly et al., 1999; *Espírito Santo–Serra dos Órgãos*) and around the São Francisco River where the Cerrado reaches the coast (IBGE, 1983; *Pernambuco–Bahia*).

In the remaining AoE boundaries, there are no longer clear barriers (*Paraná–Santa Catarina*; *Southern São Paulo–Serra do Mar of São Paulo*; *Serra do Mar of São Paulo–Southern Rio de Janeiro coast*; *Southern Rio de Janeiro coast–Serra dos Órgãos*; *Serra da Mantiqueira–Serra do Espinhaço*); this suggests that we should look for past separation events.

The Doce River was identified as a barrier by many previous studies, based on historical biogeographical (Amorim and Pires, 1996; Silva et al., 2012) and phylogeographical research (Pellegrino et al., 2005; Cabanne et al., 2007; Thomé et al., 2010; D’Horta et al., 2011), and was interpreted as the cause of separation among AoEs (Müller, 1973; Prance, 1982; Silva et al., 2004; Goldani et al., 2006). The Paraíba do Sul River was recognized as a barrier by Amorim and Pires (1996) and Pellegrino et al. (2005). Large rivers are obvious barriers, but two other types of past events may also be possible causes of separations: marine transgressions and tectonic activity. Marine transgressions resulted from Neogene climatic fluctuations during interglacial periods, and records of transgressions can reach 20 m above present sea level in Brazil since at least the early Pleistocene (Suguio et al., 2005). As rivers drained into wide valleys with lacustrine systems and marine sedimentation is noted hundreds of kilometres from the coast, transgressions have the potential to greatly affect forest biota. It is possible that transgressions influenced the colonization of the Paraíba do Sul and São Francisco valleys by open vegetation, replacing previously forested areas. Tectonic activity has occurred in these rifts since the Oligocene in the case of the Paraíba do Sul River and has been recorded since the early Quaternary for at least the Doce River (Almeida and Carneiro, 1998; Saadi et al., 2005).

The wide valley of the São Francisco River near the coast is covered by Cerrado vegetation that extends south into the Todos os Santos Bay (IBGE, 1983). Based on our results, the MRE of *Pernambuco* also reaches this bay; we thus hypothesize that the transition in physiognomy is a more important barrier than the river. Todos os Santos Bay and the Paraguaçu

River that flows into it were considered as a biotic division by previous authors (Müller, 1973; Amorim and Pires, 1996; Pellegrino et al., 2005; Silva et al., 2012).

Between the *Southern Rio de Janeiro coast* and *Serra da Bocaina*, the top of the front scarp of the Serra da Bocaina plateau has open vegetation known as ‘rocky fields’ that separates the slope forest from the plateau forest. Here the topography is directly responsible for the isolation. In the limits of other AoEs, however, the role of mountainous terrain in the disjunction of the forest biota is indirect.

The origins of mountain ranges east of the Brazilian Platform are connected with tectonic activity that started in the Palaeocene and uplifted the previously submerged continental platform adjacent to the Santos basin (Almeida and Carneiro, 1998). Similar movements occurred through the Cenozoic and formed the ‘Continental Rift System of the Serra do Mar’, which caused the parallel faults of the mountain ranges and opened the Rio Paraíba do Sul Valley and the present rough terrain (Almeida and Carneiro, 1998; Saadi et al., 2005). The Paraíba do Sul Valley separated the Serra da Mantiqueira from the Serra do Mar, Serra da Bocaina and Serra dos Órgãos mountain ranges. Other evidence for tectonism comes from taphrogenic basins such as the Guanabara Bay, Angra dos Reis Bay, Curitiba basin, São Paulo basin (Almeida and Carneiro, 1998; Saadi et al., 2005) or even Todos os Santos Bay.

These tectonic events could have affected the forest biota during catastrophic uplift events by separating some AoEs. Or they could have affected forest biota with the rough terrain causing a reduction in forest coverage on the top of mountain ranges and on wide valleys where less orographic rain occurs, as in the Paraíba do Sul and São Francisco rivers.

Given the available evidence that the present terrain is responsible for different physiognomies and the interruption of present-day forests, climatic fluctuations during the Neogene probably affected species ranges. Geological, geomorphological, palaeoclimatological, palaeopalynological and biogeographical evidence points to climatic fluctuations affecting tropical South America, with moist and warm periods alternating with dry and cold periods (e.g. Haffer, 1987; Saia et al., 2008), a reduction of forested areas and an expansion of savannahs more recently (e.g. Ledru et al., 2005). Despite several criticisms of the ‘Refuge Model’ as an explanation for the high diversity of the Amazon (e.g. Collinvaux et al., 2000), the hypothesis that forest physiognomies were greatly reduced during drier periods has found strong support. Carnaval and Moritz (2008) inferred the locations of refuges during the Last Glacial Maximum (LGM, 21 000 years ago) based on distribu-

tion modelling of the Atlantic Rain Forest biome and found at least two large refuges that are congruent with the following AoEs: *Pernambuco* and *Bahia*. Thomé et al. (2010) modelled the distribution of *Rhinella* spp. (Anura) in an LGM biome and found the ‘Pernambuco refuge’ and other refuges in the south-eastern region (larger than the AoEs found in the present). Some phylogeographical studies have also revealed demographic expansions in the Late Pleistocene that are congruent with a refuge model for the Atlantic Rain Forest (Martins et al., 2009; Thomé et al., 2010; D’Horta et al., 2011). These recent expansions resulted in MREs in our data (see discussion above). Another important issue is that climatic fluctuations should have generated more complex physiognomic scenarios in South America with asymmetry and asynchrony among different areas as evidence of moist and cold periods in the north-east (Oliveira et al., 1999).

Atlantic Rain Forest refuges are most likely to be located on mountain range slopes where forests were maintained by orographic rainfall (Haffer, 1987). Wide valleys, regions with marine sediments, tops of mountains and rain shadow regions are most likely to have experienced a reduction in forest coverage. Thus, most boundaries of our AoEs (*Paraná–Santa Catarina*; *Southern São Paulo–Serra do Mar de São Paulo*; *Serra do Mar de São Paulo–Southern Rio de Janeiro coast*; *Southern Rio de Janeiro coast–Serra dos Órgãos*; *Serra da Mantiqueira–Serra do Espinhaço*) correlate with a reduction in forest coverage, as the CCs of these AoEs are on slopes of mountain ranges.

We have used harvestmen phylogenetic hypotheses to historically relate these AoEs (DaSilva and Pinto-da-Rocha, 2011). These hypotheses suggest that those main divisions (oldest at the subfamily level) are the Doce River and near the southern portion of the state of São Paulo. Secondary divisions are the Paraíba do Sul River and Todos os Santos Bay. The divisions of southern São Paulo were also found by phylogeographical (Grazziotin et al., 2006; Batalha-Filho et al., 2010) and panbiogeographical (Silva et al., 2012) studies. There is evidence of tectonic events in this region since the Tertiary, with opening of the Ribeira do Iguaçu valley, which changed the structure of the Serra do Mar range (Suguio et al., 2005).

The divergence times of different harvestmen taxa of the Atlantic Rain Forest have not yet been provided. However, the divergence time of harvestmen sister species of the genus *Promitobates* (Gonyleptidae) has recently been estimated as 5–11 Myr based on a strict molecular clock model (Bragagnolo, Clouse & Pinto-da-Rocha, unpublished data). This estimate would minimize the role of Pleistocene refuges in causing speciation, but older and deeper climatic cooling during the Tertiary (e.g. Holbourn et al., 2013) could have

influenced it. Thus, our data are limited in pinpointing putative causal variables and the relative roles of climatic and geological events as drivers of biotic isolation. On the other hand, our inferences are very important as spatial indicators of main regions of both convergent disjunctions and stability for evolution of endemic species. Another limitation of our inferences is that congruence could be overestimated by an ‘areas of endemism/vicariance biogeography view’, which could alternatively be attributable to independent speciation cycles occurring at different time scales and could subsequently be interpreted as false congruencies (Donoghue & Moore, 2003), or even as ecological community assemblages or spatial turnovers of species in latitudinal, physiognomic and altitudinal gradients (e.g. Riddle, 1998; Di Virgilio et al., 2013).

However, the last speciation events may be too recent to be directly related to the tectonic events that uplifted the mountains. The oldest speciation events are probably associated with tectonic events or marine transgressions in valleys and the more recent divisions with Neogene refuges. An integrated explanation is needed to address the forms of diversification of the Atlantic Rain Forest biota or any continental biota. The role played by Tertiary tectonics in the separation of species can be felt millions of years later in the rough geomorphology of the Atlantic Rain Forest. Tectonics opened valleys that subsequently were transgressed by the sea and where forests may have been reduced during drier periods. Mountain uplift maintains large rivers and keep slopes moist, allowing orographic rainfall to maintain a well-developed forest, even during glacial periods. An important result of the phylogenetic relationships among areas (DaSilva and Pinto-da-Rocha, 2011) is the hypothesis of reiterative barriers (D. S. Amorim pers. comm.), i.e. barriers working in the same place but at different times and that connect or disconnect biotas and populations, such as refuges, marine transgressions and the integrated consequences of above-cited processes in shaping present harvestmen diversification. This is congruent with the possible high spatial frequency of divergence that is represented by AoEs, even with speciations in different times (as in the pseudo-congruence view; Donoghue & Moore, 2003).

Conclusion

If there were a difference in the levels of endemism of harvestmen and most other organisms of the Atlantic Rain Forest, can the AoEs proposed here be extrapolated to other taxonomic groups? Because it is possible that harvestmen have diversified much more than many other organisms and have maintained their distributions for longer periods due to their limited

capacity to disperse, one could argue that our conclusions cannot be generalized. The present AoEs mark vicariance events, or at least areas of historical isolation, in the Atlantic Rain Forest, which might have affected other taxa in different ways. While these events may have caused speciation in harvestmen, they may have caused less severe separations in other groups, for instance population isolation or unequal speciation (e.g. in the phylogeographic studies of Pellegrino et al., 2005; Graziotin et al., 2006; Cabanne et al., 2007). Therefore, we hypothesize that other taxa with biological requirements similar to harvestmen such as a dependency on moist forests and low vagility may have similar endemism patterns or population structure, for example crickets (Mello, 1994) and some frogs (Heyer and Maxson, 1983).

The CCs of our AoEs are good representations of regions of species origins in the Atlantic Rain Forest. MREs or regions between areas can represent transition zones with unique communities and high species richness in some cases because they include a mix of taxa from different origins. Some of these regions are characterized by geographical and vegetation differences compared with core areas of the Atlantic Rain Forest that allow exclusive communities to develop, such as in the Rio Doce Valley where there is a transition from the southern slope-forest and the northern wide-plain-forest. Thus, the AoEs proposed here are also important as markers of historical complexity of diversification in the Atlantic Rain Forest.

The AoEs proposed here represent the spatial partitioning of the Atlantic Rain Forest biodiversity at the species or population level over a historically wide scale. We propose this delimitation as a hypothesis to be tested with other forest taxa and using other methods (e.g. phylogeography). They can also play an important role in choosing priority areas for conservation.

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Supporting Information

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

Table S1. AoEs cited in the literature for the Atlantic Forest and their congruence with present delimitation.

Table S2. List of species used in the analysis.

Table S3. Detailed results of numerical analyses.

Fig. S1. Depiction of the cladogram resulting from parsimony analysis of endemism.

Data S1. Formal description of Areas of Endemism following International Code of Area Nomenclature (Ebach et al., 2008).