Detection of areas of endemism on two spatial scales using Parsimony Analysis of Endemicity (PAE): the Neotropical region and the Atlantic Forest

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Abstract: An important biological challenge today is the conservation of biodiversity. Biogeography, the study of the distribution patterns of organisms, is an important tool for this challenge. Endemism, the co-occurrence of several species unique to the same area, has important implications for the preservation of biodiversity, since many areas of endemism are also areas with large human impact. More rigorously defined, areas of endemism are historical units of distributional congruence of monophyletic taxa. These areas often assumed to be due to nonrandom historical events that favored conditions associated with high rates of speciation. Thus, understanding endemism and the delimitation of endemic areas has important implications for conservation. Today, most studies delimit areas of endemism by superimposing maps of distribution for various species. This approach suffers from arbitrary delimitations, however, when a great distributional data is used. In this paper we used the method of Parsimony Analysis of Endemicity (PAE) based on georeferenced quadrats in order to delimit areas of endemism. This modality of the method is important due to its testable nature and can also be used to infer area relationships. We applied the method to raw distributional data from 19 unrelated taxa to delimit general patterns of endemism in the Neotropical Region and in the Atlantic forest domain using different grid scales. Neotropical areas found are comprised over the Panama region, northern Andean region and the Atlantic forest. Atlantic forest showed a major division into two distinct components (northern x southern). Endemic areas delimited using smaller scale grids on the Atlantic forest should be considered for conservation priorities once they showed endemism at regional and local scales. The results were also compared to other studies using different taxa and methods. Finally, some considerations on the analysis scale and future perspectives of the method are presented.
Keywords: historical biogeography, endemism, PAE, South America.

Resumo: Um dos principais desafios para este século reside em impedir a perda de biodiversidade. A biogeografia é o campo das ciências biológicas que busca desvendar os padrões de distribuição dos organismos. Um conceito básico em biogeografia diz respeito à existência de áreas de endemismo, caracterizadas pela presença de espécies de distribuição restrita. Áreas de endemismo são definidas como unidades históricas de congruência distribucional entre dois ou mais táxons monofiléticos, provavelmente formadas por fatores históricos não aleatórios que definem condições específicas para elevadas taxas de especiação. Conseqüentemente, a delimitação de áreas de endemismo possui importantes implicações para a eficácia dos esforços conservacionistas. Até o momento, a maioria dos estudos tem delimitado estas áreas por meio da sobreposição de mapas de distribuição das espécies. Entretanto, esta abordagem pode acarretar delimitações arbitrárias quando analisado um amplo conjunto de dados distribucionais. No presente estudo foi utilizado método da Análise de Parcimônia de Endemismos (PAE) baseada em quadrículas georeferenciadas a fim delimitar áreas de endemismo. Este método é importante devido a sua natureza empiricamente testável, além da possibilidade de inferência dos relacionamentos históricos entre áreas endêmicas. O método foi aplicado aos dados distribucionais de 19 táxons não relacionados, de modo a definir os padrões gerais de endemismo na região de Neotropical e na Mata Atlântica utilizando diferentes tamanhos de quadrícula. Foram encontradas 13 áreas endêmicas Neotropicais, situadas sobre as regiões do Panamá, norte dos Andes e Mata Atlântica, sendo esta última composta por dois componentes distintos (Norte e Sul). As áreas de endemismo delimitadas na Mata Atlântica por meio de quadrículas menores devem ser consideradas prioritárias para conservação, uma vez que demonstraram endemismo tanto em escala regional quanto local. Os resultados foram comparados a outros estudos utilizando deferentes táxons e metodologias. Considerações gerais sobre escala de análise e perspectivas futuras são apresentadas.
Palavras-chave: biogeografia histórica, endemismo, PAE, América do Sul.

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Introduction

Perhaps the most important biological challenge today is the conservation of biodiversity. As human populations increase, so does the need for natural resources and space for that growing population. For the conservation of biological diversity, therefore, we must first understand the distributions of organisms and how and why these organisms are geographically distributed as they are. Biogeography, the study of the distribution patterns of organisms, is an important tool for this challenge.

A scientific perspective on the non-random distribution of organisms was first debated in the early 19th century with the first biogeographical map published by Lamarck and Candolle (Ebach & Goujet 2006). This non-random distribution results in a tendency for biodiversity to be concentrated in particular areas and so areas of endemism are those areas that contain a number of unique species (endemic species).

Areas of endemism are important in biogeography for two important reasons: 1) they are the biogeographical unit of analysis and are fundamental for hypotheses about the history of geographical units and their biota; 2) They include many endemic species and so these areas should be given priority for conservation efforts (Silva et al. 2004). More rigorously defined, areas of endemism are historical units of distributional congruence of monophyletic taxa (Harold & Mooi 1994). An assumption of areas of endemism is that species in the area share a unique history and therefore have similar biogeographic relationships (Linder 2001). The theory of areas of endemism is well established (Morrone 1994, Lowenberg-Neto & Carvalho 2004), while in practice, defining these areas is difficult (Axelius 1991). To date, most studies delineate these areas by using species distribution maps, yet this approach suffers due to arbitrary delineations when large datasets are used.

Parsimony Analysis of Endemicity (PAE) was developed to resolve this difficulty. PAE is a parsimonious algorithm that analyses raw distribution matrices based on species occurrences in geographical quadrants (Morrone 1994). PAE has many advantages, an important one of which is testability when using large numbers of species distributions. This is very important for comparing studies of different taxa in different regions. Also, PAE can provide hypotheses of primary homology among areas of endemism that may be further tested by the methods of cladistic biogeography (Morrone 2005).

The Neotropical Biogeographical Region, from Mexico to southern South America, comprises tremendous taxonomic and habitat diversity and a complex geological history. This region includes four major subregions: Caribbean, Amazonian, Chaco and Paraná (Morrone 2006), all of them subdivided into smaller units (areas of endemism). The Paraná subregion is of particular interest because it includes the Brazilian Atlantic Forest, which is increasingly endangered due to anthropogenic activities. Thus, we need to move quickly and efficiently to identify the problems and work towards protection of this area.

Currently, most studies of distributional patterns have included single or few taxa. The first delineations of areas of endemism in the Neotropical Region were based on birds (Cracraft 1985, Silva 1995) and primates and flies (Amorim & Pires 1996). These studies, although not based on PAE, were important because were the first to address the biogeographical structure of the region.

PAE has been used in studies of anurans, lizards and primates (Ron 2000), small mammals from the Atlantic Forest (Costa et al. 2000), birds and primates in Amazonian Forests (Silva & Oren 1996) and turtles (Ippi & Flores 2001). These studies are congruent in that they suggest that areas of endemism in the Amazonian Forest are spatially delimited by the main rivers, while the Atlantic Forest is divided into at least two areas of endemism.

While areas delimited for particular taxa may be extrapolated to other taxa, it is more sensible and efficient to include many unrelated taxa within the analysis. This approach may uncover general, wide scale patterns and the forces that favor areas of endemism, in contrast to particular patterns based only on a few groups. Here, based on several species of unrelated taxa, we use PAE to delimit areas of endemism in the Neotropical Region and in the Atlantic Forest of Brazil. We then compare these areas with those of previous studies and use these results to better understand endemism and the associated conservation problems.

Material and Methods

1. Distributional data

In this study, taxa were selected from published literature if they met three basic requirements: 1) Taxa were monophyletic; 2) The species distribution of the taxa was recently studied or reviewed; and 3) The distribution of the taxa was entirely within the region studied.

To accomplish requirement 1, preference was given to taxa with a consistent, species-level, phylogenetic hypothesis. However, some taxa here used still lack such hypothesis. In these cases, taxa were considered monophyletic based on evidences suggested in the references consulted. Requirement 2 was imposed to obtain the most complete distributional records known to date. Finally, requirement 3 assured that the distribution of the taxa considered was entirely within the region studied. This avoided the use of partial distributions and wrong interpretations of biogeographic homologies (Nihei 2006).

Here, we applied PAE to two distinct regions: Neotropical and Atlantic Forest. In the Neotropical region analysis, the previous requirements for taxa selection resulted in 19 taxa (Table 1) comprising 189 species and 10 subspecies, in a total of 1562 distributional records. Some localities were previously excluded due to imprecise information. On the other hand, Atlantic Forest analysis consisted of 98 species out of 199 used in the Neotropical analysis, in order to only consider species distributed inside the Atlantic Forest region (requirement 3).

Geographic coordinates for the locality record of each species were taken from several sources. Point localities within Brazil were found using the GeoLoc tool, available on the SpeciesLink website (http://splink.cria.org.br). Coordinates for taxa in other countries were obtained from the websites Fallingrain Global Gazetter (http://www.fallingrain.com/world) and Fuzzy Gazetteer (http://tomcatdmaweb1.jrc.it/fuzzyg/query). The species distribution data were plotted in maps using the programs ArcView GIS 3.2a (Esri 1999) and ArcGIS 9 (Esri 2004).

2. Parsimony Analysis of Endemicity (PAE)

Using georeferenced quadrats as operational geographical units (OGUs) was proposed to impose an objective method of analysing geographical distribution data (Morrone 1994). Thus, arbitrary delimitation of endemic areas is avoided and inference of primary homologies between OGUs becomes possible (Morrone 2001). Here, we followed the method described in Morrone (1994), which comprises four basic steps: 1) definition of quadrats size; 2) construction of a data matrix; 3) parsimony analysis of the distribution matrix; and 4) identification of the OGUs defined by at least two endemic species.

First, the Neotropical Region was divided in 110 quadrats of 4° x 4° (Figure 1a). Only quadrats within which species were analyzed

Table 1. List of taxa used in PAE and respectives references.

Tabela 1. Lista dos taxa utilizados na PAE e respectivas referências.

	Taxon	Rank	Reference
Arthropoda	*Adelpha cocala*	Lepidoptera	Willmott 2003
	Adelpha melona	Lepidoptera	Willmott 2003
	Charis	Lepidoptera	Hall & Harvey 2001
	Agaporomorphus	Coleoptera	Miller 2001
	Hypselotropis	Coleoptera	Mermudes 2005
	Anelosimus	Araneae	Agnarsson 2005
	Carapoia	Araneae	Huber 2005
	Oxyepoecus	Hymenoptera	Albuquerque & Brandão 2004
	Heteropachylinae	Opiliones	Mendes 2005
	Balacha	Hemiptera	Takiya & Mejdalani 2004
	Nicomia	Hemiptera	Albertson & Dietrich 2005
	Coenosopsia	Diptera	Michelsen 2001, Nihei & Carvalho 2004, Bortolanza et al. 2006
	Polietina	Diptera	Nihei & Carvalho 2005
	Pseudoptilolepis	Diptera	Schuehli & Carvalho 2005
	Serdia	Heteroptera	Fortes & Grazia 2005
Plants	*Aechmea*	Bromeliaceae	Canela et al. 2003
	Eremocaulon	Poaceae	Londoño & Clark 2002
Vertebrata	*Physalaemus*	Amphibia	Nascimento et al. 2005
	Siphlophis	Colubridae	Prudente 1998

are labeled. Next, only the Atlantic Forest ecoregion (sensu Josse et al. 2003) was considered and so it was divided in 124 quadrats of 1° x 1° (Figure 1b). This also permitted a comparison of both scales in this region.

Data matrices, instead of species and characters as in phylogenetic analysis, comprise species and quadrats. Species are synonymous with characters for delimiting and identifying quadrats. Matrices were binary coded (absence – 0, presence – 1) using *Hawth's Analysis Tool* for ArcGis 9 (http://www.spatialecology. com). An hypothetical primitive area (all species absent) was used to root the cladogram.

To find the most parsimonious geographic cladogram, a heuristic search was performed using the computer programs Nona (Goloboff 1999) and Winclada (Nixon 2002) with the following commands: hold 50000, hold/10 and mult*100. The unsupported nodes were collapsed and a strict consensus cladogram was selected for discussion. In the strict consensus cladogram, quadrats or clusters of quadrats supported by two or more endemic species (shown as synapomorphies in the cladogram) were considered endemic areas (Morrone 1994).

Databanks comprising species distributional records, as well as the corresponding data matrices used in PAE analysis are available from the corresponding author.

Results

Parsimony analysis in both data matrices (4° x 4° and 1° x 1° quadrats) resulted in 50,000 most parsimonious trees. Computer memory saturation due to multiple most parsimonious trees before the end of the heuristic search is probably explained by the few characters (taxa) that support OGUs. Given a finite amount of time, the best way to maximize the exploration of tree space was to limit the number of trees retained during branch swapping (Brower 2006). Although the strict consensus trees that we use here for discussion

represent a sample of many most parsimonious trees, the parameters used to find the shortest trees were merely operational criteria.

A strict consensus cladogram of 623 steps, consistency index = 31 and retention index = 28 resulted from the parsimony analysis of the Neotropical Region with 4° x 4° quadrats. OGUs supported by two or more endemic taxa (synapomorphies) were considered as evidence of endemism (following Morrone 1994, Figure 2). In the Neotropical Region, a total of 13 endemic quadrats (OGUs) were found (Figure 3, Table 2). In addition to six endemic areas (quadrats 18, 23, 25, 105, 106 and 109) a large area of endemism resulted from a group of seven quadrats (73, 74, 83, 84, 92, 99, 100) suggesting a hierarchical pattern of endemism in the southern Atlantic Forest. This hierarchy results from the existence of smaller endemic areas situated inside a larger endemic region, which may be subdivided according to the relationships among OGUs.

The Atlantic Forest parsimony analysis resulted in a strict consensus cladogram of 323 steps, CI = 30, RI = 20 (Figure 4). A total of 10 endemic OGUs were defined with only one pair of grouped quadrats (Figure 5, Table 3). Also, as is to be expected, the endemic quadrats on a 1° x 1° scale are situated within endemic quadrats defined in the larger scale used in previous analysis. In this sense, smaller scale grids provided a greater resolution of some Atlantic Forest endemic areas.

Discussion

In the larger scale analysis, two quadrats occur in Panama, probably due to the complex biological history of the closing of the isthmus 3.1-3.5 mya (Marko 2002). This region was previously recognized as a biogeographic node (Croizat 1958) that is indicative of endemism (Heads 2004). Many smaller endemic areas in the Panamanian region were defined for species in the plant genus *Piper* (Quijano-Abril 2006). This study found a larger number of endemic areas due to the smaller grid scale being used.
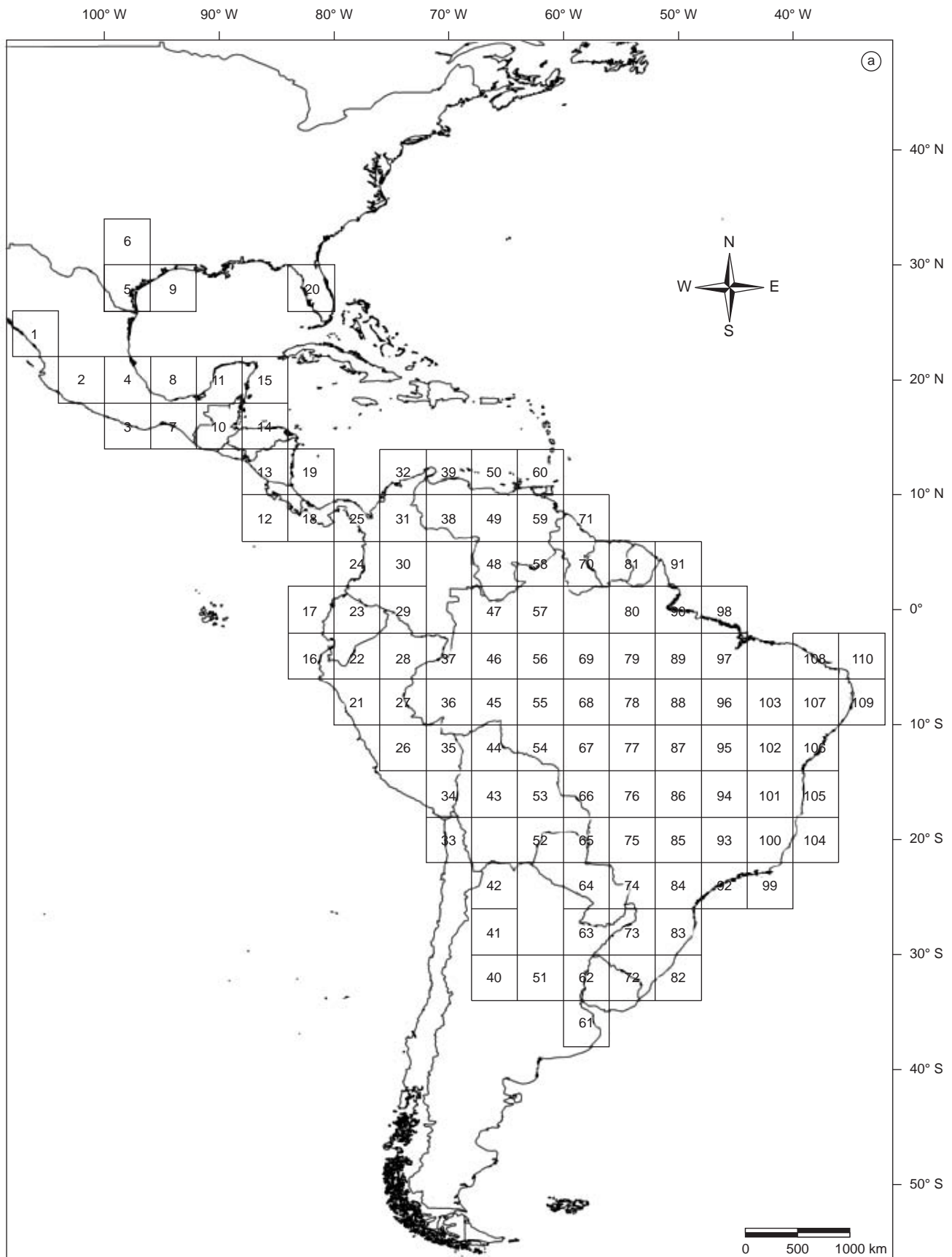
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Figure 1a. Neotropical region divided into the 4° x 4° lat/long grids for PAE analysis.

Figura 1a. Região Neotropical dividida em quadrículas de 4° x 4° lat/long para análise PAE.

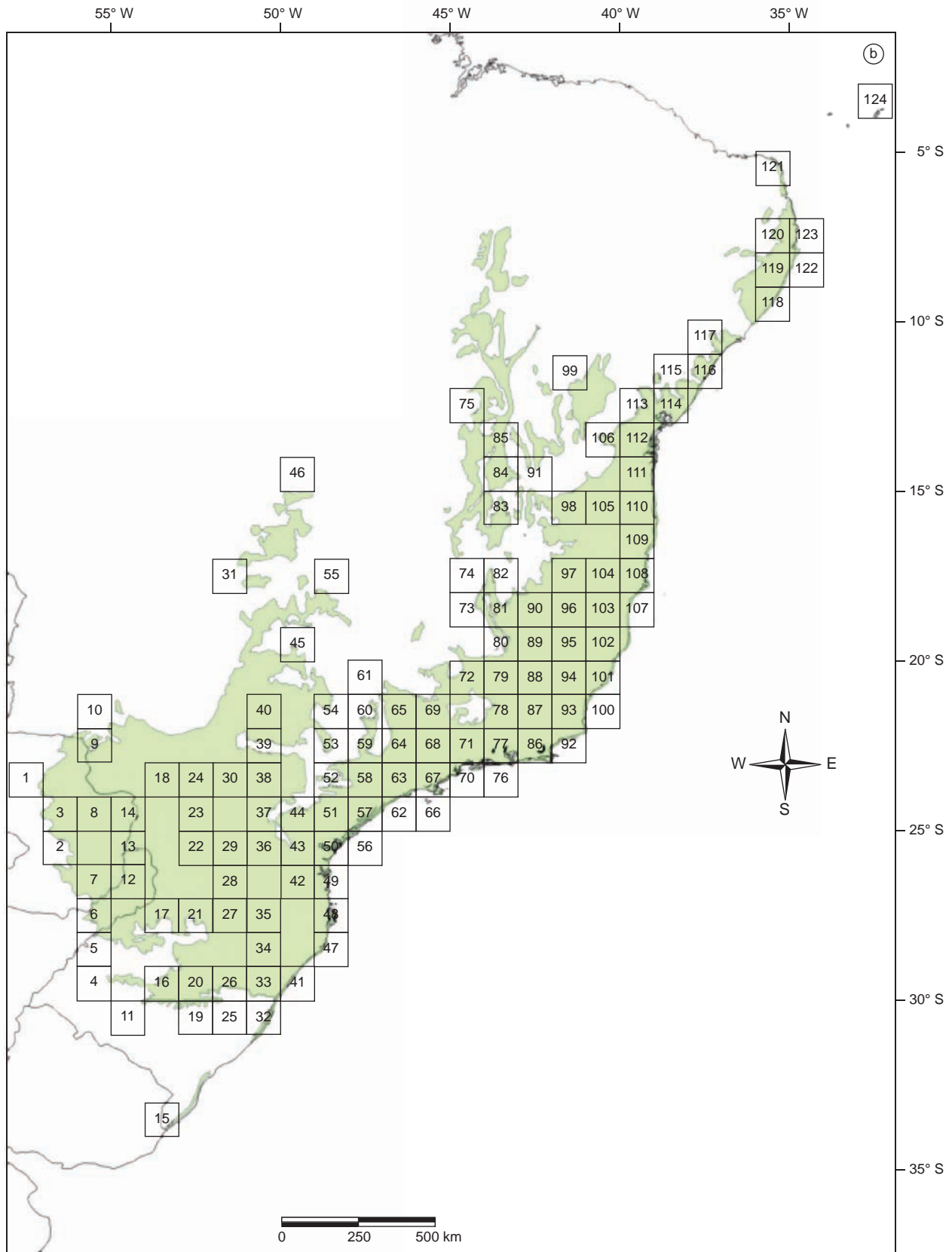Areas of endemism in the Neotropical region and Atlantic Forest

Figure 1b. Altantic forest region divided into 1° x 1° lat/long grids for PAE analysis.

Figura 1b. Região da Mata Atlântica dividida em quadrículas de 1° x 1° lat/long para análise PAE.
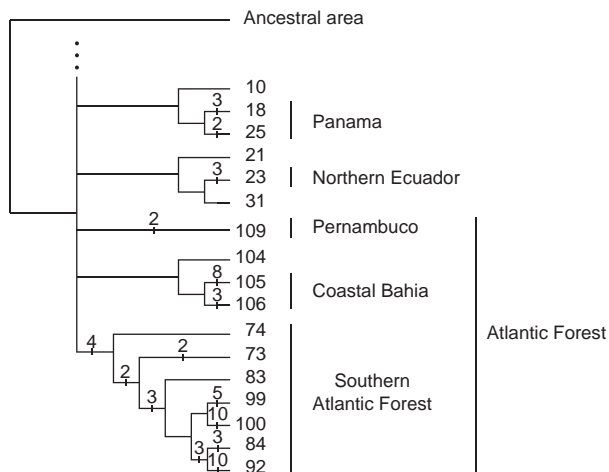
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Figure 2. Informative part of the strict consensus cladogram obtained in PAE using 4 x 4 degree lat/long grids. Internal numbers indicate the total of endemic species supporting endemic OGUs.

Figura 2. Parte informativa do cladograma de consenso estrito obtido na PAE empregando quadrículas de 4 x 4 graus (lat/long). Números internos indicam o total de espécies endêmicas suportando as quadrículas endêmicas.
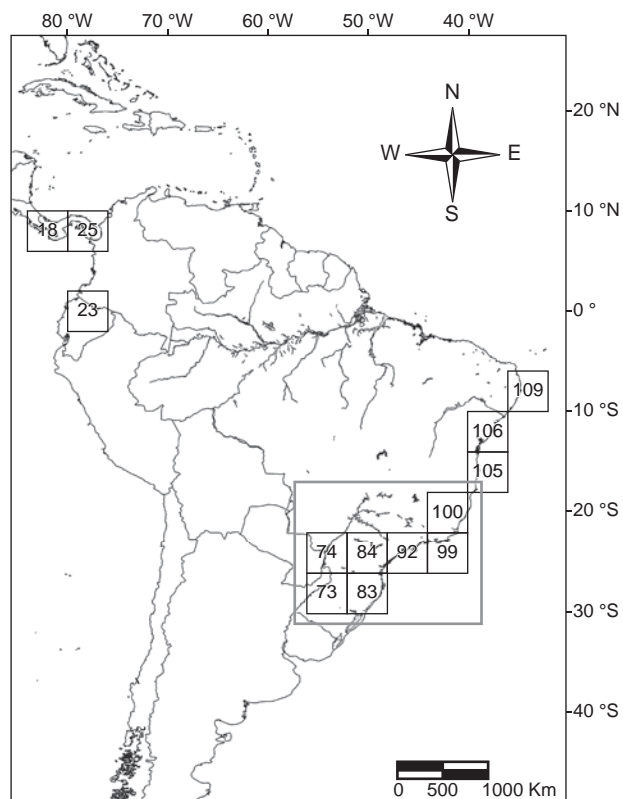

Figure 3. Endemic OGUs obtained in PAE of Neotropical region. Gray rectangle indicates grouped OGUs in Southern Atlantic Forest.

Figura 3. Quadrículas endêmicas obtidas pela PAE para a região Neotropical. O retângulo cinza indica as quadrículas agrupadas ao Sul da Mata Atlântica.

Another endemic quadrat is on the border of Colombia and Ecuador, also situated over the Andean region. This endemic area agrees with other studies that use different approaches for determining areas of endemism (Cracraft 1985, Costa et al. 2000, Morrone 2006). This region is known to favor endemism due to the altitudinal variation of the relatively recent geological formation of the Andes. Geological activity promotes speciation, which in turn tends to increase the number of endemic species (Humphries & Parenti 1999). This association between geological complexity and numbers of endemic species may be a rule for most or all areas of endemism.

The remaining areas of endemism are within the Atlantic forest domain (Figure 3). This region is well known for its many endemic species (Cracraft 1985, Amorim & Pires 1996, Costa et al. 2000, Silva et al. 2004). These areas of endemism that lie within an apparently homogeneous region suggests that historical factors (i.e., sea level fluctuations and orogeny) in the region during Pliocene-Pleistocene promoted local endemism (Rocha et al. 2005). However, a longitudinal gradient has been proposed to explain the pattern of endemism in the Atlantic Forest in which coastal areas were biogeographically distinct from the plateaus (Cracraft 1985, Morrone 2006). We believe that such a classification reflects current differences in biomes and ecology, rather than historical events, and so does not adequately explain the endemic area found here.

Hence, instead, we suggest that the data support a latitudinal trend in endemisms for this region, with support from other studies that used different analytical methods (i.e. Amorim & Pires 1996). Additionally, the southern Atlantic Forest OGUs are separated from northern areas, thereby suggesting that the Atlantic Forest comprises two divergent components of endemism (Costa et al. 2000). For example, three quadrats in the north did not group with any southern quadrats (Figure 3) and suggests a split at the state of Espirito Santo between northern and southern components (Amorim & Pires 1996). Understanding this split will require further study and probably with a finer division of quadrats. The Serra da Mantiqueira has been proposed as the location of the division between these regions (Costa et al. 2000) and almost certainly, the formation of the Valley of the Paraíba do Sul River was an important vicariant event.

In the northern Atlantic Forest, the lack of association among quadrats suggests that these endemic areas should be seen as unique, with independent histories. This pattern also finds evidence in literature, but may be confusing due to the various terminologies used when studies describe spatially congruent endemic. For example, one quadrat here was describe as "South of Bahia" by Amorim & Pires (1996), while another is located over the area southeast coast (Costa et al. 2000), coastal Bahia (Silva et al. 2004) and MGBA (Amorim & Pires 1996). Finally, an additional quadrat is associated with Pernambuco (Silva et al. 2004) and NEBR (Amorim & Pires 1996).

Conversely, the southern endemic region described here is common to most studies. While terminology may vary, spatial limits are very similar. Our cladogram due to PAE indicates a hierarchic structure for southern Atlantic forest defined by endopatry (Espinosa et al. 2001). This pattern of nested areas of endemism is important for two reasons. First, it suggests evidence for hierarchical schemes of area classifications (see Morrone 2006) and second, it provides a hypothesis for the primary homology of the relationships among areas. This hypothesis for primary homology can then be tested using the phylogenetic information of the groups involved, in a cladistic biogeography approach.

The PAE analysis with 4° x 4° OGUs was only able to detect endemic areas in parts of the Neotropical Region of South America. We wonder why endemism was undetected in the Amazonian region and Brazilian Cerrado. To answer this question, grid scale and number of taxa being analysed must be taken into account. To detect

Table 2. List of taxa supporting endemic 4 x 4 degrees OGUs.

Tabela 2. Lista espécies que suportam as quadrículas endêmicas de 4 x 4 graus.

Table 2. Continued...

OGU	Species
18	*Charis nicolayi*
	Nicomi buccina
	Pseudoptilolepis centralis
23	*Hypselotropis subnittata*
	Nicomia harenosa
	Physalaemus coloradorum
25	*Adelpha melona neildi*
	Nicomia negrescens
73	*Anelosimus missiones*
	Anelosimus rabus
84	*Balacha lépida*
	Balacha rubripennis
	Coenosopsia albuquerquei
92	*Agaporomorphus mecolobus*
	Balacha distincta
	Carapoia genitalis
	Carapoia ubatuba
	Eremocaulon setosum
	Physalaemus atlanticus
	Physalaemus barrioi
	Physalaemus bokermanni
	Pseudoptilolepis latipalpis
	Serdia maculata
99	*Anelosimus sumisolena*
	Nicomia interrupta
	Nicomia lemniscata
	Nicomia monticola
	Physalaemus soaresi
100	*Balacha caparao*
	Chavensicola inexpectabilis
	Heteropachylus sp. n. 2
	Oxyepoecus browni
	Physalaemus deimaticus
	Physalaemus erithros
	Physalaemus evangelistae
	Physalaemus maximus
	Physalaemus obtectus
	Physalaemus rupestris

OGU	Species
195	*Aechmea depressa*
	Carapoia brescovitti
	Carapoia rheimsae
	Carapoia una
	Heteropachylus sp. n. 1
	Heteropachylus perachii
	Physalaemus erikae
	Serdia costalis
106	*Carapoia crasto*
	Chavensicola crassicalnei
	Heteropachylus spiniger
109	*Physalaemus caete*
	Psudopucrolia incerta
(84, 92)	*Physalaemus moreirae*
	Physalaemus spiniger
	Pseudoptilolepis chrysella
(83, 84, 92, 99, 100)	*Adelpha cocala caninia*
	Physalaemus olfersii
	Serdia lobata
(73, 83, 84, 92, 99, 100)	*Nicomia subfasciata*
	Serdia inspersipes
(73, 74, 83, 84, 92, 99, 100)	*Oxyepoecus punctifrons*
	Polietina univittata
	Serdia calligera
	Serdia maxima

endemism using PAE it is necessary that species (characters) support areas. Considering the scale of the entire Neotropical Region, detection of endemic 4° x 4° OGUs requires a larger number of species than we used here.

Interestingly, larger grid sizes should have resulted in more endemic OGUs because they would include more endemic species. However, since 5 degrees of latitude is approximately 550 km, larger grid sizes will often result in grouping different ecosystems in the same area of endemism (Morrone & Escalante 2002) and causing confusion in the biological interpretation of such distributions. On the other hand, decreasing grid size, as in the analysis of the Atlantic

Forest, endemism was not shown in some previously considered areas of endemism in the 4° x 4° analysis. Because the detection of endemic areas is scale dependent, additional studies should address this issue by using many different quadrat sizes. This is especially important for the conservation of biological diversity, since precision is desirable.

It is also interesting to note that in PAE based on quadrats, OGU size does not need to be the same. Although a few studies have tried this variable quadrat size approach (i.e. Morrone & Escalante 2002), it offers important applications for cladistic biogeography, which demands the indication of endemic areas for all taxa analyzed
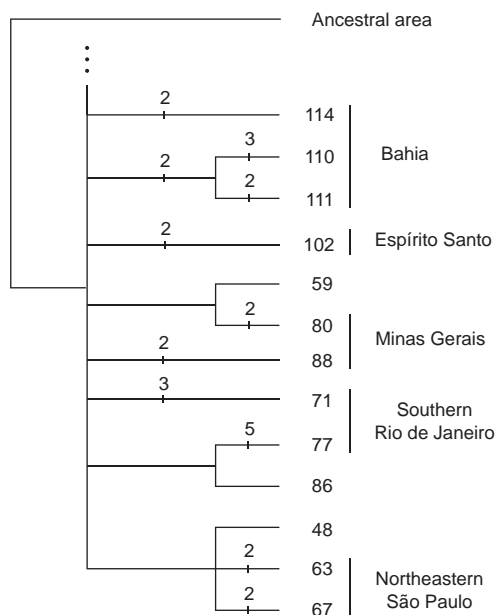
Figure 4. Informative part of the strict consensus cladogram from PAE using 1° x 1° lat/long grids of the Atlantic Forest. Numbers on the branches indicate the total number of endemic species supporting the endemic OGU.

Figura 4. Parte informativa do cladograma de consenso estrito obtido na PAE empregando quadrículas de 1 x 1 graus (lat/long) na Mata Atlântica. Números internos indicam o total de espécies endêmicas suportando as quadrículas endêmicas.
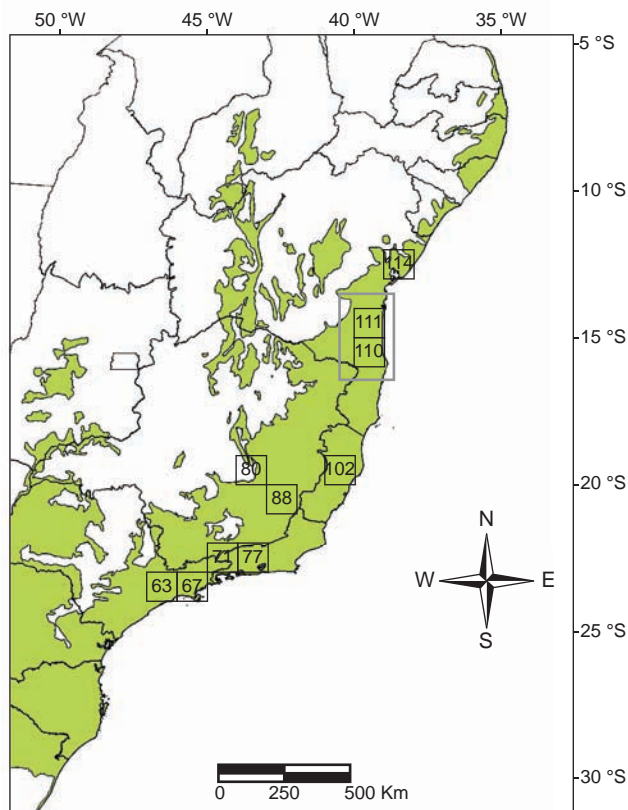

Figure 5. Endemic OGUs from PAE of the Atlantic Forest region with the grouped OGUs (within rectangle) in the southern coast of the State of Bahia, Brazil.

Figura 5. Quadrículas endêmicas obtidas pela PAE na região da Mata Atlântica, mostrando ainda o agrupamento das quadrículas localizadas no litoral Sul do Estado da Bahia (retângulo).

Table 3. List of taxa supporting endemic 1 x 1 degrees OGUs.

Tabela 3. Lista de espécies que suportam as quadrículas endêmicas de 1 x 1 grau.

Quadrat	Species
63	*Physalaemus bokermanni*
	Pseudoptilolepis latipalpis
67	*Carapoia ubatuba*
	Physalaemus atlanticus
71	*Balacha distincta*
	Physalaemus barrioi
	Serdia maculata
77	*Anelosimus sumisolena*
	Nicomia interrupta
	Nicomia lemniscata
	Nicomia monticola
	Physalaemus soaresi
80	*Physalaemus deimaticus*
	Physalaemus evangelistae
88	*Balacha caparao*
	Physalaemus maximus
102	*Heteropachylus* sp. n. 2
	Physalaemus obtectus
110	*Carapoia brescovitti*
	Carapoia una
111	*Heteropachylus perachii*
	Serdia costalis
114	*Chavensicola crassicalnei*
	Heteropachylus spiniger
(110, 111)	*Aechmea depressa*
	Heteropachylus sp. n. 1

(Humphries & Parenti 1999). Moreover, it may be used to define endemic areas using PAE even when a small number of taxa is analyzed. For example, consider the analysis here made using 4° x 4° OGUs. In order to delimit endemic areas all over South America using the same number of taxa, endemic OGUs defined at 4° x 4° may be kept and, in a second analysis, the remain region divided in grids of 5° x 5°, followed by a new analysis. This cycle is repeated many times, maintaining the size of endemic grids defined at a given scale and increasing grid size on the remaining areas for a new round of parsimony analysis. The analysis continues until all of the areas of endemism in South America are delimited.

Based on our results, we recommend the use of smaller grid sizes for more precision and better biological concordance with distribution data. However, the quality of the results will depend on the number of species being analysed, and that will require additional research about species distribution. This requirement is not unique to PAE, but rather is important in all biogeographic methods. Thus, distribution information from biological collections should be rapidly computerized and made widely available as a priority to better understand the patterns of biological diversity and its conservation. Efforts are being made in this direction and must be encouraged (i.e. CRIA - http://www.cria. org.br/). Besides, more reliable distributional data should be addressed by increasing the sampling effort on poorly studied groups.

Conservation implications from this study are that areas indicated in the 1° x 1° analysis should be regarded as priorities for conservation, since these quadrats demonstrate historical endemism at both local and regional scales. PAE analysis using quadrats is shown to be a strong tool for biogeographic analysis because the method is

easily applied, tested and the results can be fine-tuned as more data become available (Silva et al. 2004).

The cladograms show little information about endemic area relationships, since most of the taxa used did not cluster OGUs. The only inference we were able to make is that some areas of the Atlantic forest were grouped, suggesting the presence of two distinct components (northern and southern). The use of PAE to infer area homology and relationships is still being debated in literature (Brooks & Van Veller 2003, Santos 2005, Nihei 2006). The critiques directed to PAE are basically due to absence of phylogenetic information, what may lead to false relationships among areas. Besides, *static* PAE (see Nihei 2006) suffers from the lack of temporal information, leading to conclusions based on distributional data from a single geological horizon. On the other hand, Morrone (2001) claimed that the establishment of homology should follow a two step program, in which PAE would be responsible for formulating a first hypothesis of area relationships.

Considering the wide variety of approaches available for biogeographic analysis (Crisci et al. 2003), it seems reasonable to not discard any method until well established comparisons can be made. Fortunately, this will lead to a more complete picture of the biotic evolution in the Neotropical regions.

Acknowledgements

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