Endemism analysis of Neotropical Pentatomidae (Hemiptera, Heteroptera)

Augusto Ferrari[1], Andressa Paladini[2], Cristiano Feldens Schwertner[3] & Jocelia Grazia[1]

1. Laboratório de Entomologia Sistemática, Departamento de Zoologia, Programa de Pós-Graduação em Biologia Animal, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves, 9500, Bloco IV, prédio 43435, 91501-970 Porto Alegre, RS, Brazil. (ferrariaugusto@gmail.com; jocelia@ufrgs.br)
2. Departamento de Zoologia, Programa de Pós-Graduação em Entomologia, Universidade Federal do Paraná, Caixa Postal 19020, 81531-980 Curitiba, PR, Brazil. (andri_bio@yahoo.com.br)
3. Departamento de Ciências Biológicas, Universidade Federal de São Paulo, Campus Diadema, Rua Prof. Artur Riedel, 275, 09972-270, Diadema, SP, Brazil. (acrosternum@yahoo.com.br)

ABSTRACT. The definition of areas of endemism is central to studies of historical biogeography, and their interrelationships are fundamental questions. Consistent hypotheses for the evolution of Pentatomidae in the Neotropical region depend on the accuracy of the units employed in the analyses, which in the case of studies of historical biogeography, may be areas of endemism. In this study, the distribution patterns of 222 species, belonging to 14 Pentatomidae (Hemiptera) genera, predominantly neotropical, were studied with the Analysis of Endemicity (NDM) to identify possible areas of endemism and to correlate them to previously delimited areas. The search by areas of endemism was carried out using grid-cell units of 2.5° and 5° latitude-longitude. The analysis based on groupings of grid-cells of 2.5° of latitude-longitude allowed the identification of 51 areas of endemism, the consensus of these areas resulted in four clusters of grid-cells. The second analysis, with grid-cells units of 5° latitude-longitude, resulted in 109 areas of endemism. The flexible consensus employed resulted in 17 areas of endemism. The analyses were sensitive to the identification of areas of endemism in different scales in the Atlantic Forest. The Amazonian region was identified as a single area in the area of consensus, and its southeastern portion shares elements with the Chacoan and Paraná subregions. The distribution data of the taxa studied, with different units of analysis, did not allow the identification of individual areas of endemism for the Cerrado and Caatinga. The areas of endemism identified here should be seen as primary biogeographic hypotheses.

KEYWORDS. Areas of endemism, NDM, Atlantic Rain Forest, Amazonian region, grid-cells.

RESUMO. Análise de endemismo de táxons neotropicais de Pentatomidae (Hemiptera: Heteroptera). A definição de áreas de endemismo é central aos estudos de Biogeografia Histórica e suas inter-relações são questões fundamentais. Hipóteses consistentes sobre a evolução de Pentatomidae (Hemiptera) na Região Neotropical dependem da acuidade das unidades empregadas nas análises, que no caso de estudos de biogeografia histórica, podem ser áreas endêmicas. Neste trabalho foram estudados os padrões de distribuição de 222 espécies, pertencentes a 14 gêneros de Pentatomidae, com ocorrência predominantemente neotropical, com base em uma Análise de Endemicidade (NDM) a fim de inferir possíveis áreas endêmicas e relacioná-las a áreas previamente delimitadas. A busca por áreas endêmicas foi realizada com quadrículas de 2,5° e 5° latitude-longitude. A análise com base em agrupamentos de 2,5° latitude-longitude permitiu identificar 51 áreas de endemismo, sendo que o consenso destas áreas resultou em quatro agrupamentos de quadrículas. A segunda análise, com quadrículas de 5° latitude-longitude, resultou em 109 áreas de endemismo. O consenso flexível empregado resultou em 17 áreas de endemismo. As análises foram sensíveis à identificação de áreas de endemismo na Mata Atlântica em diferentes escalas. A região Amazônica foi identificada como uma área única no consenso, sendo que a porção sudeste compartilha elementos com as sub-regiões do Chaco e Paraná. Os dados de distribuição dos táxons estudados, com diferentes unidades de análises, não permitiram a identificação de áreas endêmicas para o Cerrado e a Caatinga. As áreas de endemismo aqui identificadas devem ser tratadas como hipóteses biogeográficas primárias.

PALAVRAS-CHAVE. Áreas endêmicas, NDM, Mata Atlântica, região amazônica, quadrículas.

The definition of areas of endemism is central to studies of historical biogeography, and the relationships among them are fundamental questions (Nelson & Platnick, 1981; Henderson, 1991). In a way analogous to phylogenetic systematics, in which species or supra-specific taxa are grouped, units in biogeography are grouped as areas of endemism (Linder, 2001). An area of endemism can be diagnosed through evaluation of the overlapping of the distribution areas of two or more species (Platnick, 1991; Morrone, 1994). However, as this overlapping is never total, somehow the identification of areas of endemism might be a subjective procedure. Assuming that these areas are the basic units of the historical biogeographic analysis, their definition, conceptual as well as methodological, play an essential role in biogeographic analyses (Platnick, 1991; Linder,

2001). According to Cavieres et al. (2002), the use of areas of endemism in the identification of areas for conservation makes possible to identify priority areas not based only on the generally used criteria, such as species diversity and richness.

According to Morrone (2009), areas of endemism (or biotic elements) share a common history but may not represent monophyletic entities, due to events of reticulation caused by geographic dispersion or biogeographic convergence. The conformation of the areas can be the result of historical factors, associated with vicariance events, or a combination of ecologic factors that limit the area of occurrence of the taxa (Nelson & Platnick, 1981; Hovenkamp, 1997; Laffan & Crisp, 2003). The processes associated with dispersal presuppose that the organisms have a particular history

through a stable geography. In this context, the spatial conformation of the distribution is due to the similar response of organisms to geographic barriers, where these organisms are confined to these areas. The vicariance process assumes that areas of endemism are formed from ancestral distribution areas, which fragment with the appearance of barriers, thereby dividing the biota into subpopulations, with different dispersal and colonizing capacities (Espinosa *et al.*, 2001).

The methods in vicariance or cladistic biogeography assume that the limits of the distribution of species originating in the same area of endemism should be in general more congruent among themselves than with those of species originating in other areas of endemism (Hausdorf, 2002). In this context, the vicariance model presupposes that the limits of species distribution are not random (Morrone, 1994; Hausdorf, 2002). Based on these premises, we can hypothesize that the distribution of species showing some level of congruence can be the result of a close relation between the history of the earth and the history of the biotas (Croizat, 1964), which can allow to infer a particular pattern.

Morrone (2001) proposed two steps in the identification of areas of endemism: primary biogeographic homology, which refers to a conjecture on a common biogeographic history, inferred from different taxa integrated in spatial-temporal manner in a biota; and the secondary biogeographic homology, with regard to the use of cladistic results to test the primary homologies. Cladistic biogeography allows us to compare different area cladograms, by the substitution of the taxa by the areas of endemism in which they occur, making it possible to construct general hypotheses of the relation of the areas or general area cladograms (Nelson & Platnick, 1981; Humphries & Parenti, 1999). Different delimitations of areas of endemism can result in contradictory hypotheses of area relationships, as result of the substitution of the terminals by areas of occurrence, for the same collection of data analyzed (Henderson, 1991; Hausdorf, 2002).

Szumik *et al.* (2002) and Szumik & Goloboff (2004) proposed a method for identifying areas of endemism, which takes into consideration the spatial position of the localities of the taxa, and makes it possible to group grid-cells (areas of endemism) based on indices (scores) of the endemic species of these grid-cells. The score of endemism of an area of endemism (cluster of grid-cells) is the result of the sum of the scores of endemism of the species that occur in these grid-cells.

In a comparative study with different methodologies for searching areas of endemism, involving 609 species of plants with occurrence in the archipelago of Canary Islands, Carine *et al.* (2009) evaluated the performance of hierarchical methods such as parsimony analysis of endemicity (PAE) and UPGMA, relative to analysis of endemicity (NDM: eNDeMism) proposed by Szumik *et al.* (2002) and Szumik & Goloboff (2004). According to these authors, the search algorithm NDM was superior to the hierarchical methods in number of areas found that satisfied the criteria used, and in the total areas found. Then, it is preferable to incorporate spatial information in

the delimitation of the areas and accept overlapped areas of endemism.

The use of grid-cells in biogeographic studies is a frequent procedure, where their size is defined according to the area of study and the density of the distribution data of the taxa studied. The definition of the grid-cells can vary considerably, from restricted areas with a unit of 0.5° (Cavieres *et al.*, 2002; Rovito *et al.*, 2004) to 1° (Sigrist & Carvalho, 2008) to 2.5° (Linder, 2001) and to 5° for continental areas (Costa & Leite, 2000; Goldani *et al.*, 2002; Biondi & D'Alessandro, 2006). Larger grid-cells can include a higher number of single species and result in areas with greater support. However, using larger grid-cells increases the probability of including areas with greater heterogeneity of ecosystems, which can obscure possible biological patterns in grouping areas with little support (Morrone & Escalante, 2002; Sigrist & Carvalho, 2008).

Insects are especially important in studies that attempt to answer biogeographic questions and to understand global patterns of distribution, either by the age of the taxa or the diversity of species. The lack of knowledge of the distribution and phylogeny of the insects, and their high diversity has hampered the use of this group of organisms in biogeographic studies (Morrone, 2006). Works on the identification of areas of endemism with data for Hemiptera include studies with PAE in Cercopidae and Membracidae (Goldani *et al.*, 2002; Goldani & Carvalho, 2003) and in Heteroptera with Peiratinae (Reduviidae) (Morrone & Coscarón, 1996), besides a panbiogeographic analysis of the genus *Pselliopus* Bergroth (Reduvidae: Harpactorinae) (Marino-Perez *et al.*, 2007). Morrone *et al.* (2004) used a panbiogeographic analysis to study the distribution patterns of 60 species of Belostomatidae, Corixidae, Micronectidae and Gerridae for the Chaco region. Sigrist & Carvalho (2008) conducted a PAE with 19 unrelated taxa, and included data of *Serdia* Stål, 1867 (Heteroptera, Pentatomidae). Thomas (2000) reviewed the literature and summarized the knowledge of the pentatomids occurring in Mexico. Based on the limits of distribution of these taxa, a classification of the biotic elements was proposed: Nearctic, Holarctic, Pan-Tropical and Neotropical, including in this last element a classification for endemic species of Mexico, where it recognizes nine biotic provinces selected among the 18 established by Goldman & Moore (1945) based on vertebrates.

In this paper the distribution patterns of 14 predominantly Neotropical Pentatomidae (Hemiptera) genera were studied with the application of the Analysis of Endemicity (NDM) proposed by Szumik *et al.* (2002) and Szumik & Goloboff (2004), to recognize areas of endemism and to relate them to previously delimited areas.

MATERIAL AND METHODS

The groups included in the analysis were selected based on the following criteria: predominantly Neotropical distribution, recent taxonomic revision, with hypothesis of monophyly, and studies with detailed distribution information. Species with uncertain taxonomic position, subspecies, and species or specimens with incomplete

or incongruent distribution data were not included in the analysis.

The latitude and longitude of the respective localities were defined according to the following databases: Global Gazetteer version 2.1 (FALLING RAIN GENOMICS, 2007), Species Link - GeoLoc (CRIA, 2007) and GLOSK (2008).

The analysis included 222 species (Appendix I), belonging to 14 genera of Pentatomidae, with a total of 1932 georeferenced points. Of the total species included, 50 had only one distribution point sampled. Among the species with only one locality surveyed, some are only known by the holotype, incomplete data or incongruent labeling. These species with single localities, despite not directly influencing the grouping of grid-cells, were included in the analysis, because they are covered in the fourth criterion proposed by SZUMIK et al. (2002) and can affect the indices of the areas.

The genera included in the analysis were the following (classification of the subfamilies and tribes according to Rider, 2009): *Adevoplitus* Grazia & Becker, 1995 (5 spp.; Pentatominae: Pentatomini); *Agroecus* Dallas, 1851 (6 spp.; Pentatominae, Carpocorini), *Antiteuchus* Dallas, 1851 (38 spp.; Discocephalinae, Discocephalini), *Arocera* Spinola, 1837 (9 spp.; Pentatominae, Catacanthini), *Brachystethus* Laporte, 1833 (9 spp.; Edessinae), *Cataulax* Spinola, 1837 (5 spp.; Discocephalinae, Discocephalini), *Chinavia* Orian, 1965 (67 spp.; Pentatominae, Nezarini), *Dichelops* Spinola, 1837 (13 spp.; Pentatominae, Carpocorini), *Evoplitus* Amyot & Serville, 1843 (1 sp.; Pentatominae, Pentatomini), *Pallantia* Stål, 1862 (4 spp.; Pentatominae, Pentatomini), *Pseudevoplitus* Ruckes, 1958 (3 spp.; Pentatominae, Pentatomini), *Rio* Kirkaldy, 1909 (17 spp.; Pentatominae, Menidini), *Serdia* Stål, 1860 (18 spp.; Pentatominae, Pentatomini), and *Thyanta* Stål, 1862 (27 spp.; Pentatominae, "unplaced") (list of species: see Appendix I).

Chinavia is composed of 84 species, where 13 are Afrotropical, two Nearctic, and 69 registered for South America. They are polyphagous and are reported to be associated with more than 30 families of plants (SCHWERTNER & GRAZIA, 2006). Some species are pests of important crops, such as *Chinavia acuta* (Dallas, 1851) in Africa, *C. hilaris* (Say, 1831) in the United States and Canada and *C. impicticornis* (Stål, 1872) in Brazil (MCPHERSON & MCPHERSON, 2000; PANIZZI et al., 2000). The monophyly of the genus was established by SCHWERTNER (2005). The distribution data for *Chinavia* species and the respective localities were retrieved from ROLSTON (1983), RIDER (1986), RIDER & ROLSTON (1987a), SCHWERTNER (2005), SCHWERTNER & GRAZIA (2006) and GRAZIA et al. (2006).

BARCELLOS & GRAZIA (2003a), in a cladistic analysis of 10 species of *Brachystethus* and genera included in Edessinae, demonstrated its monophyly and transferred the genus to this subfamily. Also, a biogeographic hypothesis for the genus was proposed, and associated some of the resulted dichotomies with vicariance events of the Cretaceous for the Neotropical region. The distribution data for the nine species included in *Brachystethus* were retrieved from BARCELLOS & GRAZIA (2003b).

The distribution data for *Serdia*, a monophyletic genus that currently comprises 18 species, were retrieved from FORTES & GRAZIA (2005), who revised the genus and inferred its monophyly based on a cladistic analysis.

GRAZIA (1997), in a cladistic analysis of the group *Evoplitus* – which includes *Evoplitus*, *Pseudoevoplitus* and *Adevoplitus* – corroborated the monophyly of the group and of the genera included. The localities of the nine species included were retrieved from GRAZIA et al. (1993; 1994), GRAZIA & BECKER (1995) and GRAZIA et al. (2002).

Dichelops was reviewed by GRAZIA (1978) and its monophyly supported, including 14 species; the data referring to the localities were retrieved from the material examined (GRAZIA, 1978).

The South American species of the genus *Thyanta* were studied by RIDER & CHAPIN (1991). In a subsequent study, RIDER & CHAPIN (1992) reviewed 14 species from North America, Central America and Antilles. The 27 Neotropical species were included in the analysis and the distribution data were retrieved from both.

The other species and respective localities analyzed were obtained from the following taxonomic revisions: *Pallantia* (GRAZIA, 1980), *Agroecus* (RIDER & ROLSTON, 1987b), *Arocera* (RIDER, 1992), *Rio* (GRAZIA & FORTES, 1995; FORTES & GRAZIA, 2000), *Cataulax* (GRAZIA et al., 2000), and *Antiteuchus* (FERNANDES & GRAZIA, 2006).

The search by areas of endemism was carried out using grid-cell units of 2.5° and 5° latitude-longitude. The two groups of grid-cells generated for Latin America and Caribbean islands were initiated at -124.306° longitude and -41.474° latitude. The areas analyzed include the Mexican Transition Zone, Neotropical region, South American Transition Zone and Andean region. The areas were compared with the classification proposed by MORRONE (2006) (Fig.1).

Analysis of endemism (NDM/VNDM). The score of endemism of the species is defined based on four criteria (SZUMIK et al., 2002; SZUMIK & GOLOBOFF, 2004). The first is the most restrictive, requiring total spatial congruence of the distribution of the species in the cluster of grid-cells in question, and when satisfied it is the one that most contributes to the score of the area. The second criterion does not require that all the species have identical distributions to contribute to the score of the area, where they can occur in grid-cells adjacent to the area in question. The third does not require that all the grid-cells of the area in question have the same composition of species, but only the species that occur in all the grid-cells contribute to the index. The fourth criterion takes into consideration, for the calculation of the score, the species absent in one or some of the grid-cells of the area in question.

The algorithm used for calculation of the scores of endemicity include the following steps (SZUMIK et al., 2002; SZUMIK & GOLOBOFF, 2004): 1. Plot the localities of the species on a map with grid-cells. 2. Calculate the endemicity values for all possible groupings of grid-cells, considering the scores of the endemic species of these areas (clusters) in accordance with the four criteria defined by SZUMIK et al. (2002). 3. Choose the groupings of grid-cells with score of endemism greater than 2. 4. Visualize
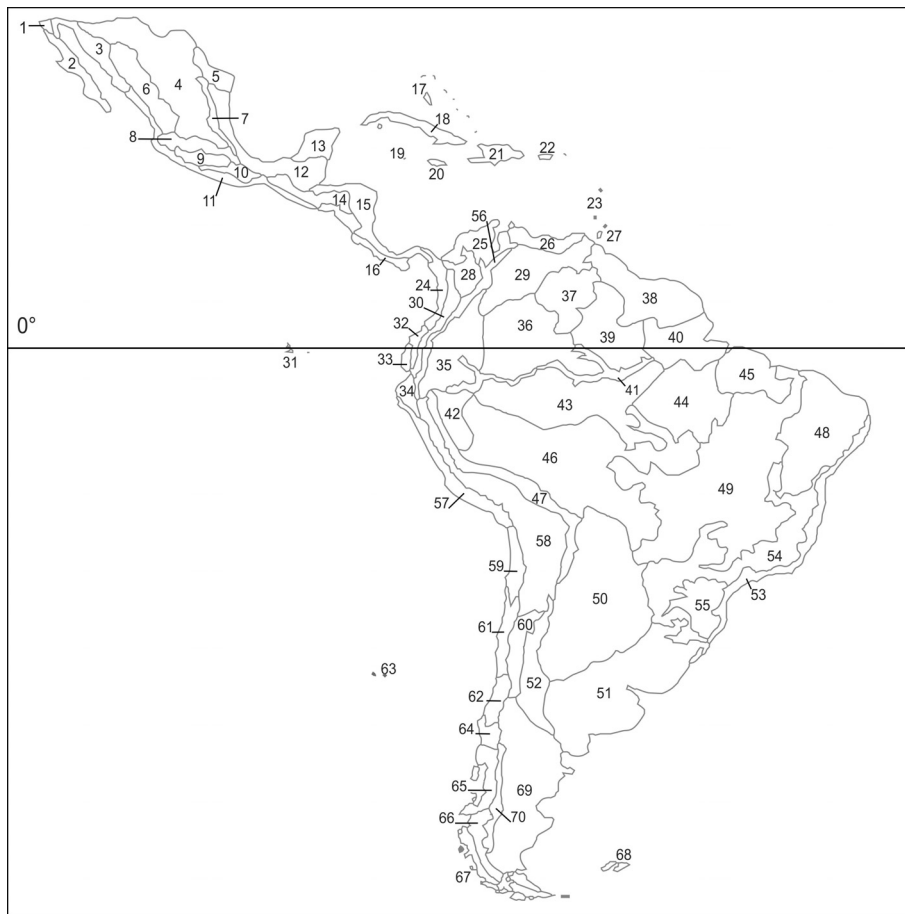
Figure 1. Biogeographic classification of Latin America and the Caribbean islands: 1, California; 2, Baja California; 3, Sonora; 4, Mexican Plateau; 5, Tamaulipas; 6, Sierra Madre Occidental; 7, Sierra Madre Oriental; 8, Transmexican Volcanic Belt; 9, Balsas Basin; 10, Sierra Madre del Sur; 11, Mexican Pacific coast; 12, Mexican Gulf; 13, Yucatan Peninsula; 14, Chiapas; 15, eastern Central America; 16, western Panamanian Isthmus; 17, Bahamas; 18, Cuba; 19, Cayman Islands; 20, Jamaica; 21, Hispaniola; 22, Puerto Rico; 23, Lesser Antilles; 24, Choco; 25, Maracaibo; 26, Venezuelan coast; 27, Trinidad and Tobago; 28, Magdalena; 29, Venezuelan Llanos; 30, Cauca; 31, Galapagos Islands; 32, western Ecuador; 33, arid Ecuador; 34, Tumbes-Piura; 35, Napo; 36, Imeri; 37, Guyana; 38, Humid Guyana; 39, Roraima; 40, Amapá; 41, Várzea; 42, Ucayali; 43, Madeira; 44, Tapajós-Xingu; 45, Pará; 46, Pantanal; 47, Yungas; 48, Caatinga; 49, Cerrado; 50, Chaco; 51, Pampa; 52, Monte; 53, Brazilian Atlantic forest; 54, Paraná Forest; 55, *Araucaria angustifolia* Forest; 56, North Andean Paramo; 57, coastal Peruvian Desert; 58, Puna; 59, Atacama; 60, Prepuna; 61, Coquimbo; 62, Santiago; 63, Juan Fernandez Islands; 64, Maule; 65, Valdivian forest; 66, Magellanic forest; 67, Magellanic Paramo; 68, Malvinas Islands; 69, Central Patagonia; 70, Subandean Patagonia (Morrone, 2006).

the groupings of grid-cells (areas of endemism) on a map. 5. Apply a criterion of consensus, when necessary, for the purpose of synthesize the information contained in clusters of similar grid-cells (with respect to composition of endemic species and grid-cells included) in an area of consensus.

In the present study, the areas of endemism were identified according to the concept of Platnick (1991), who assumed that the more or less congruent limits of distribution of two or more species represent areas of endemism. Obviously, in this context, congruence does not imply an exact overlapping of the limits for all the possible scales of cartographic representation, but rather a relative sympatry at the level of resolution desired for analysis (Platnick, 1991).

The method to search the areas of endemism was carried out with the program NDM v. 2.6 (Goloboff, 2008) and visualized with VNDM (Goloboff, 2008).

The options of heuristic searches were carried out keeping areas with at least two endemic species and score of endemism over 2. The option of permutation of one grid-cell each time was used. The randomization parameter of the searches was defined as zero ("random seed" = 0). We did not use the filling option, which uses a ray from the points recorded on the map for defining the presence of species in the grid-cells. The absence of species was not inferred for grid-cells which did not have occurrence data. The calculation of the scores of the areas of endemism took into consideration the proportion of grid-cells that limited them.

The parameters of heuristic search used in the analysis were modified in comparative tests to estimate their effect on the results obtained. The results were little affected by the search parameters, where the consensus of the resultant areas remained unchanged.

The areas of endemism found by the search criterion of the NDM resulted in some cases in overlapping areas that differed with respect to the presence of a/some grid-cell(s) or endemic species(s). The areas of consensus summarize the information contained in these individual areas that share a certain

percentage of endemic species, facilitating the comparison and discussion of the results, mainly when the number of resultant areas is very high. The flexible consensus was applied, with 40% minimal similarity of endemic species for the grouping of areas initially found, in the analyses with units of grid-cells of 2.5° and 5° latitude-longitude. The results of the flexible consensus also included individual areas (single) found by the initial analysis, when these did not satisfy the criteria employed in the consensus.

RESULTS

The analysis based on groupings of grid-cells of 2.5° of latitude-longitude allowed the identification of 51 areas of endemism, with scores of endemism varying from 2.00 to 8.057. The consensus of these areas resulted in four clusters of grid-cells (Figs 2-5).

Area 1 (Fig. 2) formed by two disjunct grid-cells situated in northern Colombia and northeastern Venezuela, included in the Caribbean sub-region, and within the Northwestern South American domain. Similar

results were found in both analysis (grid-cells of 2.5° and 5°), showing the same species for areas 1 and 8 (Tab. I). Area 1 contains *Thyanta obtusa* Rider, 1991 and *T. sinuata* Rider, 1991, both with endemicity score of 1, as a result of spacial congruence in the two grid-cells.

Forty six areas are related to the grid-cells situated in the Atlantic Forest biogeographic province, and included in the consensus of area 2 (Fig. 3), with 28 endemic species (Tab. I). The grid-cells with greater score of endemism, varying from 7.220 to 8.057, are composed by species that occur predominantly in the Brazilian Atlantic Forest and *Araucaria angustifolia* Forest. With exception of *Chinavia longicorialis* (Breddin, 1901) - Pampa, *C. obstinata* (Stål, 1860) - Pampa, *Serdia inspersipes* Stål, 1860 - Pampa, and *Dichelops avilapiresi* Grazia, 1978 - Chaco, this area of consensus corresponds to the portion with the greatest score of endemism of area 13 (Fig. 14), in the analysis with grid-cells of 5°, in the Atlantic Forest domain.

Two areas of endemism (not represented graphically) were found with scores varying from 2.43 to 2.73, occurring in different portions of the Atlantic Forest
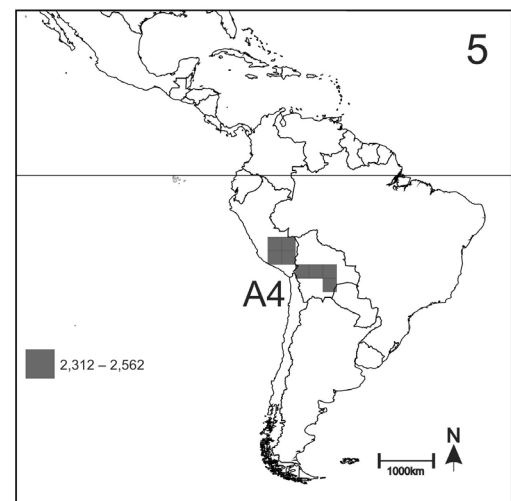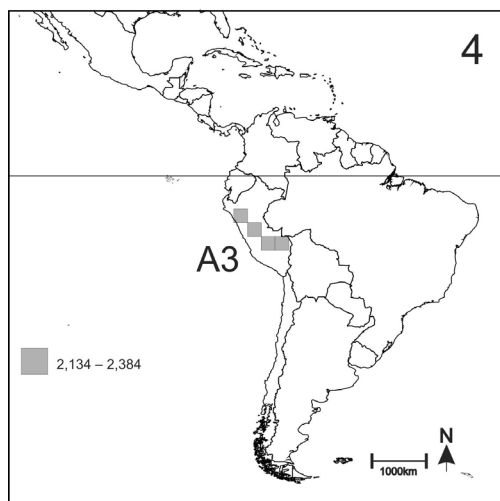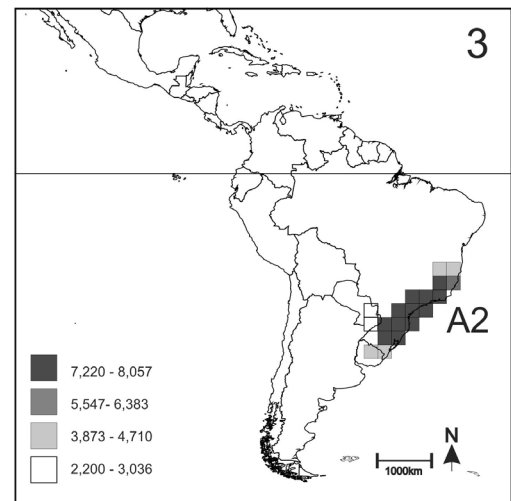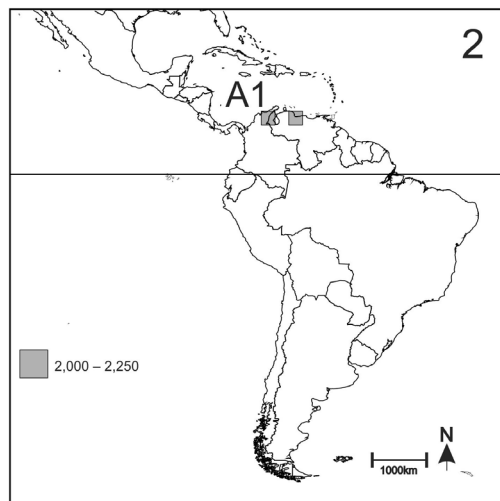
Figures 2-5. Consensus of the areas of endemism resulting from the analysis based on grid-cells of 2.5° latitude-longitude: 2, area 1; 3, area 2; 4, area 3; 5, area 4 (for endemic taxa of the areas and respective scores of endemism, see table I).

and not included in the consensus of area 2 (Fig. 3) by the criterion used. One of these areas is formed by a grouping of five grid-cells, situated between Espírito Santo and northern Paraná. The second area is composed of the grouping of 10 grid-cells, extending from northeastern Uruguay up to southern Paraná.

Area 3 (Fig. 4) is formed by four grid-cells, situated on a diagonal in the southeast/northeast direction in Peru, sharing two of the three endemic species found in area 10 (Fig. 11) with grid-cells of 5°.

Area 4 (Fig. 5) is composed of three endemic species, covering eight grid-cells situated in southern Peru and southeastern Bolivia, and sharing the presence of *Thyanta boliviensis* Rider, 1991 with area 9 (grid-cells with 5°- Fig. 10). Areas of endemism 3 and 4 are located predominantly in the Yungas province (Tab. I), which belongs to the Amazonian Subregion. Area 3 also includes portions at the extreme north of the Puna province, and area 4 extends to the southeast, forming clusters that overlap in 2 grid-cells, but showing a distinct composition of species (Tab. I).

The second analysis searched for groups of grid-cells with two or more endemic species, with analysis units of 5° latitude-longitude, and resulted in 109 areas of endemism. The highest index of endemicity of the initial cluster was 20.08, for an area with four grid-cells found in the Atlantic Forest and included in the consensus of area 13 (Fig. 14). The flexible consensus employed resulted in 17 areas of endemism (Figs. 6-22).

Consensus area 5 (Fig. 6) results from six initial clusters encompassing 12 endemic species (Tab. I). The area is situated predominantly in the Mesoamerican domain, including all its provinces. The consensus area even includes the provinces of the Mexican transition zone, with *Arocera melanopyga* Stål, 1858 and *Chinavia solita* Rider & Rolston, 1986 in the Sierra Madre Oriental, with *A. melanopyga* Stål, 1858 and *Brachystethus rubromaculatus* Dallas, 1851 in the Sierra Madre del Sur provinces; and in the Nearctic region, *Antiteuchus innocens* Engleman, 1976 with distribution in the south of the Mexican Plateau province.

Areas 6 (Fig. 7), 7 (Fig. 8) and 8 (Fig. 9) show occurrence between the limits south of the Mesoamerican domain and northeast of the Antillean domain; area 6 is composed of four endemic species, area 7 of three and area 8 of six (Tab. I).

Area 9 (Fig. 10), with four endemic species, occur in the South American transition zone provinces (Coastal Peruvian Desert, Puna and Atacama) and *Thyanta boliviensis* Rider, 1991 to the south of Yungas (Amazonian subregion). Area 10 (Fig. 11) with six endemic species - two of *Thyanta* and two of *Serdia* (Tab. I) – encompasses the provinces of Tumbes-Piura, Napo, Yungas and North Andean Paramo.

Area 11 (Fig. 12) consists of 12 grid-cells and 12 endemic species, two shared with area 9 and two with area 10, with *Thyanta xerotica* Rider, 1991 being common to the three areas (Tab. I). The area results from the consensus of six groupings of the initial search, with limits on the north and south corresponding to those of areas 9 and 10. Area 11 includes areas 3 and 4, resulting from the search with grid-cells of 2.5°, showing variation

in the scores of endemism for the species included in the groupings (Tab. I).

Area 12 (Fig. 13) is composed of eight grid-cells containing four endemic species (Tab. I) in the provinces of Yungas (to the south) and Chaco (to the extreme west) and in the South American transition zone (Monte, Prepuna and Puna) and Andean region (Coquimbo, Santiago and north of Central Patagonia).

Consensus area 13 (Fig. 14) is the result of 58 initial clusters of grid-cells and integrates 56 species (Tab. I). Consensus area 13 has a wide geographic range in the analyzed area and includes the greater part of the groupings initially found in the analysis of 5° (58 of 109 groupings). This result can be a consequence of the type of consensus employed, of overlapping areas of endemism or even of taxa with wide distribution. The groupings initially found, which compose the consensus area 13, varied from 4 to 13 grid-cells, with scores of endemism between 2.21 and 20.08. The consensus area is composed predominantly by species of *Chinavia* (19 spp.), *Serdia* (9 spp.), *Dichelops* (8 spp.), *Thyanta* (5 spp.) and *Agroecus* (3 spp.). Altogether, these five genera encompass 44 species and a large part of the diversity of area 13. Consensus area 13 includes the following provinces: Pantanal province, to the south and southeast; the south of Yungas province; all the provinces of the Chacoan subregion, with the Caatinga at least to the extreme south and Cerrado to the southeast; the provinces of the Paraná subregion, with the species that most contributed to the scores of endemism of the consensus occurring in this area; in the South American transition zone, the extreme east of the Puna and Prepuna provinces, and in the Andean region, the Santiago and Central Patagonia provinces.

Area 14 (Fig. 15) is composed of eight endemic species, situated in the Parana subregion provinces, a portion to the south of Cerrado and to the extreme east of Pantanal provinces (Tab. I). Area 15 (Fig. 16) shows 11 endemic species, where three are shared with area 14 and seven with area 13.

The Atlantic Forest biogeographic province was identified by other clusters of grid-cells, besides those included in consensus 13, 14 and 15. Area of endemism 16 (Fig. 17) is composed of three widely distributed species, including several biogeographic provinces (Tab. I). Area 17 (Fig. 18) is constituted by three endemic species, two of these not occurring in area 13, including all the Paraná subregion and the limits on the east of Chaco, Pampa, Cerrado and Caatinga.

The second area in number of groupings included in the consensus was area 18 (Fig. 19), resulting from 18 groupings of the initial search and with 21 endemic species (Tab. I). Area 18 corresponds to the Amazon Forest biogeographic province, and the initial clusters of grid-cells that resulted in this area, varied from 4 to 14 grid-cells. There was a considerably distinct composition of species and geographic position, from well centralized areas (grid-cells with higher score of endemism of Fig. 19) to groupings restricted to the south, southwest or east of the consensus. *Antiteuchus* contributed most to the definition of the area, with 12 species, followed by *Chinavia* (4 spp.) and *Rio* (2 spp.). The area of endemism

18 includes all provinces of the Amazonian subregion, with the exception of Guyana and Yungas, and includes even a portion of northeastern Cerrado, which belongs to the Chacoan subregion.

Area 19 (Fig. 20), with four endemic species, is formed by 10 grid-cells in two disjunct groupings, with the portion to the northeast composed of six grid-cells in the Amazon region, including Guyana, Várzea, Amapá,
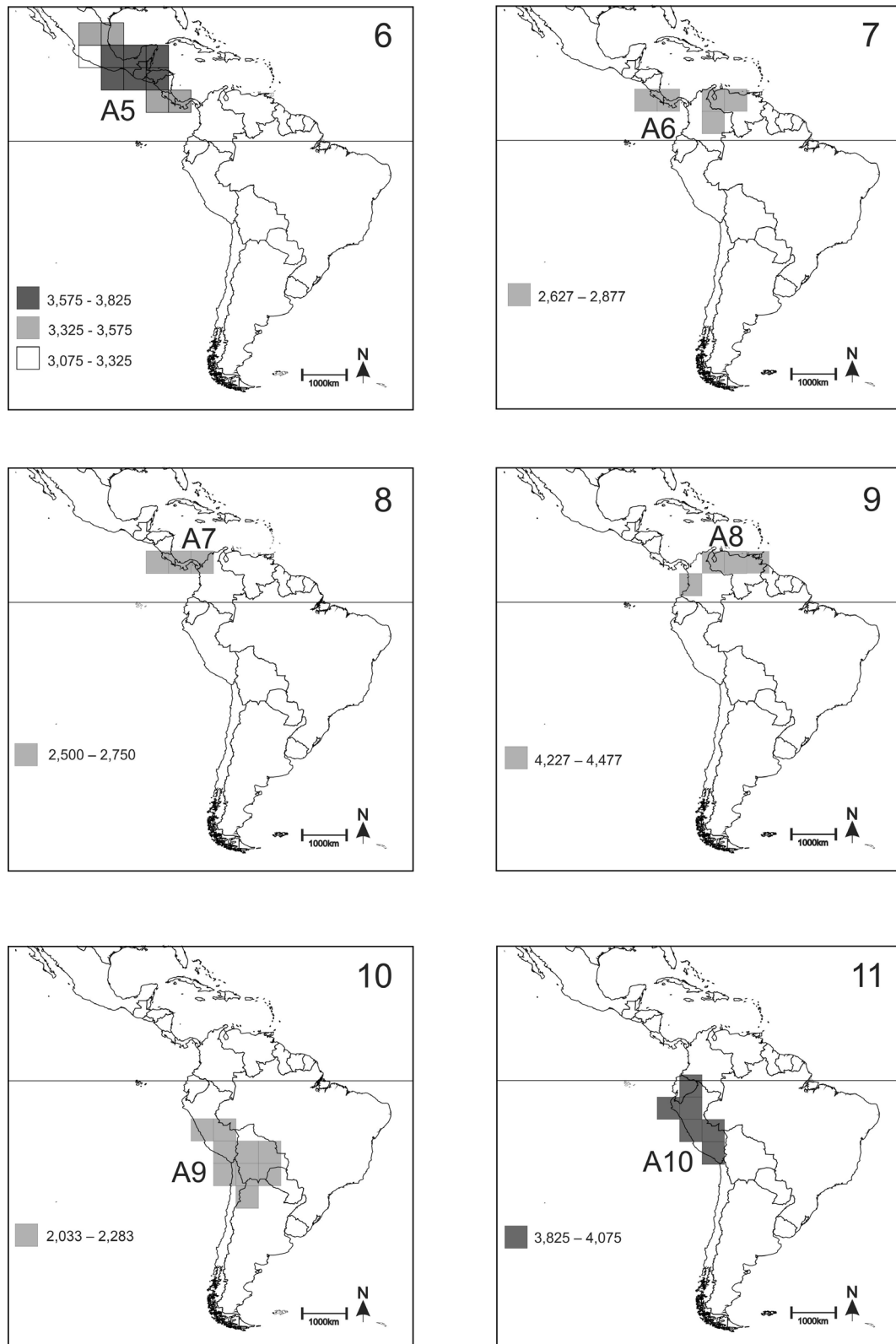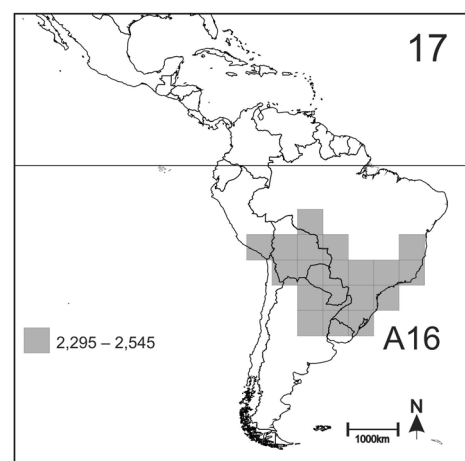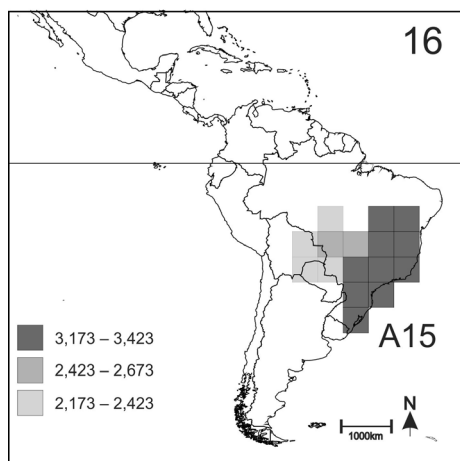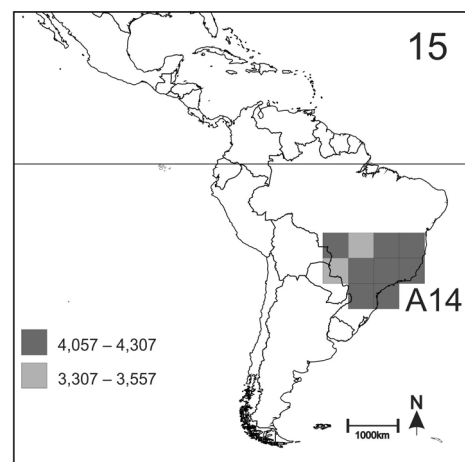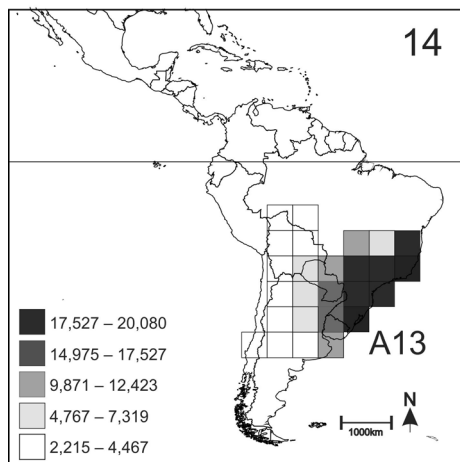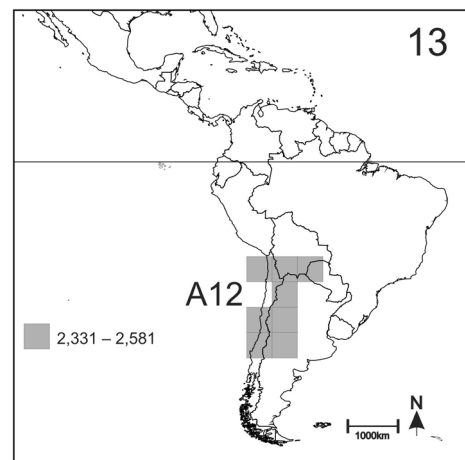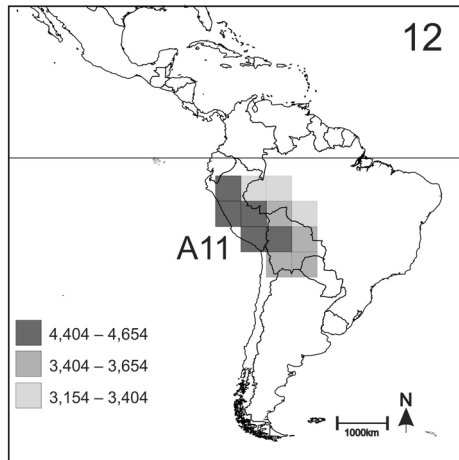

Figures 6-11. Consensus of the areas of endemism resulting from the analysis based on grid-cells of 5° latitude-longitude: 6, area 5; 7, area 6; 8, area 7; 9, area 8; 10, area 9; 11, area 10 (for endemic taxa of the areas and respective indices of endemism, see table I).

Table I. Areas of endemism identified in the analysis of 2.5° (areas 1-4) and 5° latitude - longitude (areas 5-21) and respective endemic species. The numbering of the biogeographic provinces corresponds to figure 1. Areas partially overlapping the biogeographic provinces are indicated by the portion occupied in parentheses, with the following notation: N, north; S, south; E, east; W, west.

| Endemic area	Biogeographic provinces (Morrone, 2006) included in the areas of endemism	Endemic species included in the areas of endemism (indices of endemism between parentheses)
A1 (Fig. 2)	25, 26	*Thyanta obtusa* (1.000); *Thyanta sinuata* (1.000).
A2 (Fig. 3)	53, 54, 55	*Agroecus brevicornis* (0.000-0.714); *A. scabricornis* (0.000-0.682); *Antiteuchus nebulosus* (0.000-0.667); *A. radians* (0.000-0.778); *A. tesselatus* (0.000-0.667); *Cataulax eximius* (0.000-0.740); *Chinavia brasicola* (0.000-0.750); *C. difficilis* (0.000-0.682); *C. esmeralda* (0.000-0.750); *C. longicorialis* (0.000-0.553); *C. obstinata* (0.000-0.639); *C. pontagrossensis* (0.000-0.667); *C. geniculata* (0.000-0.643); *Dichelops avilapiresi* (0.000-0.735); *D. punctatus* (0.000-0.857); *Evoplitus humeralis* (0.000-0.746); *Pallantia macula* (0.000-0.875); *Serdia apicicornis* (0.000-0.786); *S. bicolor* (0.000-0.625); *S. calligera* (0.000-0.729); *S. concolor* (0.000-0.900); *S. inspersipes* (0.000-0.686); *S. lobata* (0.000-0.750); *S. maxima* (0.000-0.586); *S. robusta* (0.000-0.786); *Thyanta fimbriata* (0.000-0.714); *T. robusta* (0.000-0.643).
A3 (Fig. 4)	47, 58 (N)	*Antiteuchus peruensis* (0.635); *Serdia quadridens* (0.750); *S. ruckesi* (0.750).
A4 (Fig. 5)	47	*Agroecus ecuadoriensis* (0.688); *Brachystethus vexillum* (0.750); *Thyanta boliviensis* (0.875).
A5 (Fig. 6)	4 (S) – 7 – 8 – 9 – 10 – 11 – 12 – 13 – 14 – 15 – 16	*Adevoplitus mexicanus* (0.000-0.800); *Antiteuchus costaricensis* (0.000-0750); *A. innocens* (0.000-0.929); *Arocera melanopyga* (0.000-0.232); *Brachystethus rubromaculatus* (0.000-1.000); *Chinavia scutellata* (0.000-0.714); *C. solita* (0.000-0.525); *C. triangula* (0.000-0.667); *Rio obscuratus* (0.000-0.667); *R. testaceus* (0.000-1.000); *R. variegatus* (0.000-0.643); *Serdia beckerae* (0.000-0.750).
A6 (Fig. 7)	15 (S) – 16 – 25 – 26 – 29 (N) – 56	*Brachystethus improvisus* (0.655); *Cataulax pudens* (0.700); *Chinavia ista* (0.700); *Rio insularis* (0.573).
A7 (Fig. 8)	15 (S) – 16	*Antiteuchus costaricensis* (0.833); *Chinavia macdonaldi* (0.833); *Serdia beckerae* (0.833).
A8 (Fig. 9)	25 – 26 – 29 (N) – 56	*Brachystethus signoretii* (0.614); *Rio insularis* (0.614); *Thyanta obtusa* (0.750); *T. testacea* (0.750); *T. sinuata* (0.750); *T. vadosa* (0.750).
A9 (Fig. 10)	47 (S) – 57 – 58 – 59	*Chinavia chilensis* (0.625-0.700); *Thyanta boliviensis* (0.000-0.813); *T. rubicunda* (0.596-0.677); *T. xerotica* (0.000-0.677).
A10 (Fig. 11)	34 – 35 – 47 (N) – 56 (S) – 58 (N)	*Antiteuchus pictus* (0.677); *Chinavia plaumanni* (0.667); *Serdia quadridens* (0.667); *S. ruckesi* (0.667); *Thyanta hamulata* (0.545); *T. xerotica* (0.614).
A11 (Fig. 12)	42 – 46 – 47 – 57 – 58 – 59	*Agroecus ecuadoriensis* (0.625-0.700); *Antiteuchus graziae* (0.000-0.536); *A. mimeticus* (0.000-0.643); *A. peruensis* (0.000-0.700); *A. variegatus* (0.000-0.489); *Brachystethus vexillum* (0.688-0.800); *Chinavia chilensis* (0.000-0.700); *C. occulta* (0.000-0.667); *Serdia quadridens* (0.000-0.700); *S. ruckesi* (0.000-0.700); *Thyanta boliviensis* (0.533-0.857); *T. xerotica* (0.000-0.485).
A12 (Fig. 13)	47(S) – 50(W) – 52 – 58 – 60 – 61 – 62 – 69 (N)	*Chinavia apicicornis* (0.563); *Dichelops lobata* (0.625); *Thyanta acutangula* (0.563); *T. rubicunda* (0.582).
A13 (Fig. 14)	46 – 47 (S) – 48 (S) – 49 (S) – 50 – 51– 52 – 53 – 54 – 55 – 58(E) – 60 – 62 – 69 (N)	*Agroecus brevicornis* (0.000-0.750); *A. lizerianus* (0.000-0.700); *A. scabricornis* (0.000-0.875); *Antiteuchus nebulosus* (0.000-0.750); *A. radians* (0.000-0.875); *Brachystethus geniculatus* (0.000-0.744); *Catalaux eximius* (0.000-0.833); *Chinavia apicicornis* (0.000-0.563); *C. armigera* (0.000-0.750); *C. aseada* (0.000-0.613); *C. australe* (0.000-0.658); *C. brasicola* (0.000-0.750); *C. callosa* (0.000-0.700); *C. difficilis* (0.000-0.900); *C. esmeralda* (0.000-0.750); *C. erythrocnemis* (0.000-0.889); *C. geniculata* (0.000-0889); *C. herbida* (0.000-0.700); *C. longicorialis* (0.000-0.750); *C. musiva* (0.000-0.628); *C. obstinata* (0.000-0.611); *C. occulta* (0.000-0.667); *C. pengue* (0.000-1.000); *C. pontagrossensis* (0.000-0.611); *C. rideri* (0.000-0333); *C. sebastiaoi* (0.000-0.875); *Dichelops avilapiresi* (0.000-0.800); *D. furcatus* (0.000-0.332); *D. lobatus* (0.000-0.700); *D. melacanthus* (0.000-0.846); *D. phoenix* (0.000-0.671); *D. pradoi* (0.000-0.667); *D. punctatus* (0.000-0.875); *D. saltensis* (0.000-0.643); *Evoplitus humeralis* (0.000-0.875); *Pallantia macula* (0.000-1.000); *P. macunaima* (0.000-0.700); *Pseudoevoplitus paradoxus* (0.000-0.656); *Serdia apicicornis* (0.000-0.875); *S. bicolor* (0.000-0.750); *S. calligera* (0.000-1.000); *S. concolor* (0.000-0.800); *S. indistincta* (0.000-0.750); *S. limbatipennis* (0.000-0.800); *S. lobata* (0.000-1.000); *S. maxima* (0.000-0.850); *S. robusta* (0.000-1.000); *Thyanta acuminata* (0.000-0.788); *T. aeruginosa* (0.000-0.667); *T. boliviensis* (0.000-0.563); *T. fimbriata* (0.000-0.875); *T. humilis* (0.000-0.850); *T. robusta* (0.000-0750).
A14 (Fig. 15)	46 – 48 (S) – 49 –53 – 54 – 55	*Arocera acroleuca* (0.288-0.625); *Chinavia obstinata* (0.404-0.580); *C. rideri* (0.635-0.643); *Dichelops phoenix* (0.370-0.536); *D. pradoi* (0.000-0.688); *Pallantia macunaima* (0.000-0.625); *Serdia inspersipes* (0.519-0.696); *S. maxima* (0.404-0.580).
A15 (Fig. 16)	46 (S) – 47 (S) – 48 (S) – 49 – 50 (N) – 51 (NE) – 53 – 54 – 55	*Arocera acroleuca* (0.000-0.833); *A. spectabilis* (0.000-0.677); *Brachystethus geniculatus* (0.000-0.719); *Cataulax eximius* (0.000-0.750); *Chinavia immaculata* (0.000-0.611); *C. rideri* (0.000-0.778); *Dichelops pradoi* (0.000-0.667); *D. phoenix* (0.000-0.696); *D. saltensis* (0.000-0.625); *Serdia indistincta* (0.000-0.592); *Thyanta acuta* (0.000-0.570).
A16 (Fig. 17)	46 (S) – 47 (S) – 49 (S) – 50 – 51 (N) – 53 – 54 – 55 – 58 (E)	*Dichelops furcatus* (0.472); *Thyanta acuminata* (0.575); *T. acuta* (0.684); *T. braziliensis* (0.564).
A17 (Fig. 18)	48 – 49 (E) – 50 (E) – 51 (NE) – 53 – 54 – 55	*Arocera spectabilis* (0.792); *Brachystethus geniculatus* (0.833); *Chinavia nigridorsata* (0.729).
A18 (Fig. 19)	35 – 36 – 39 – 40 (S) – 41 – 42 (E) – 43 – 44 – 45 (E) – 46 – 49 (NE)	*Antiteuchus beckerae* (0.000-0.578); *A. doesburgi* (0.000-0.667); *A. exiguus* (0.000-0.750); *A. geometricus* (0.000-0.750); *A. graziae* (0.000-0.657); *A. ledeburi* (0.000-0.643); *A. pallescens* (0.000-0.731); *A. punctissimus* (0.000-0.714); *A. rideri* (0.000-0.643); *A. schuhi* (0.000-0.722); *A. simulatus* (0.000-0.722); *A. variegatus* (0.000-0.722); *Cataulax subtiliterconspersus* (0.000-0.786); *Chinavia gravis* (0.000-0.567); *C. occulta* (0.000-0.700); *C. pecosa* (0.000-0.643); *C. vanduzeei*

Tab. I (cont.)

		(0.000-0.638); *Dichelops leucostigmus* (0.000-0.622); *Pseudoevoplitus vitattus* (0.000-0.700); *Rio clipeatus* (0.000-0.700); *R. punctatus* (0.000-0.667).
A19 (Fig. 20)	37 – 41 – 44 – 49 – 53 – 54 (SE)	*Antiteuchus rideri* (0.532); *Brachystethus vicinus* (0.700); *Dichelops leucostigmus* (0.700); *D. nigrum* (0.510).
A20 (Fig. 21)		*Antiteuchus mixtus* (0.602-0.726); *A. tripterus* (0.000-9.761); *Chinavia impicticornis* (0.536-0.658); *C. runaspis* (0.629-0.684); *T. perditor* (0.000-0.684).
A21 (Fig. 22)		*Antiteuchus macraspis* (0.534); *A. tripterus* (0.645); *Arocera apta* (0.595); *Thyanta perditor* (0.714).

Figures 12-17. Consensus of the areas of endemism resulting from the analysis based on grid-cells of 5° latitude-longitude: 12, area 11; 13, area 12; 14, area 13; 15, area 14; 16, area 15; 17, area 16 (for endemic taxa of the areas and respective scores of endemism, see table I).

Tapajós-Xingu and east of the Pará province. The portion to the south of the area is constituted by four grid-cells in the central region and southeast of the Cerrado, Brazilian Atlantic Forest and Paraná Forest. All species included in area 19 occur in both disjunct portions, but *Brachystetus vicinus* Signoret, 1851 and *Dichelops leucostigmus* (Dallas, 1851) were the species that contributed most to the scores of the grouping (Tab. I).

Areas 20 (Fig. 21) and 21 (Fig. 22), with five and four endemic species respectively, result in wide areas between parallels 11°N and 28°S and 11°N and 33°S. These areas include all the provinces of the Neotropical region and the portions to the east of Puna province, which belong to the South American transition zone. These areas differ in the following: area 21 includes the Western Panamanian Isthmus,
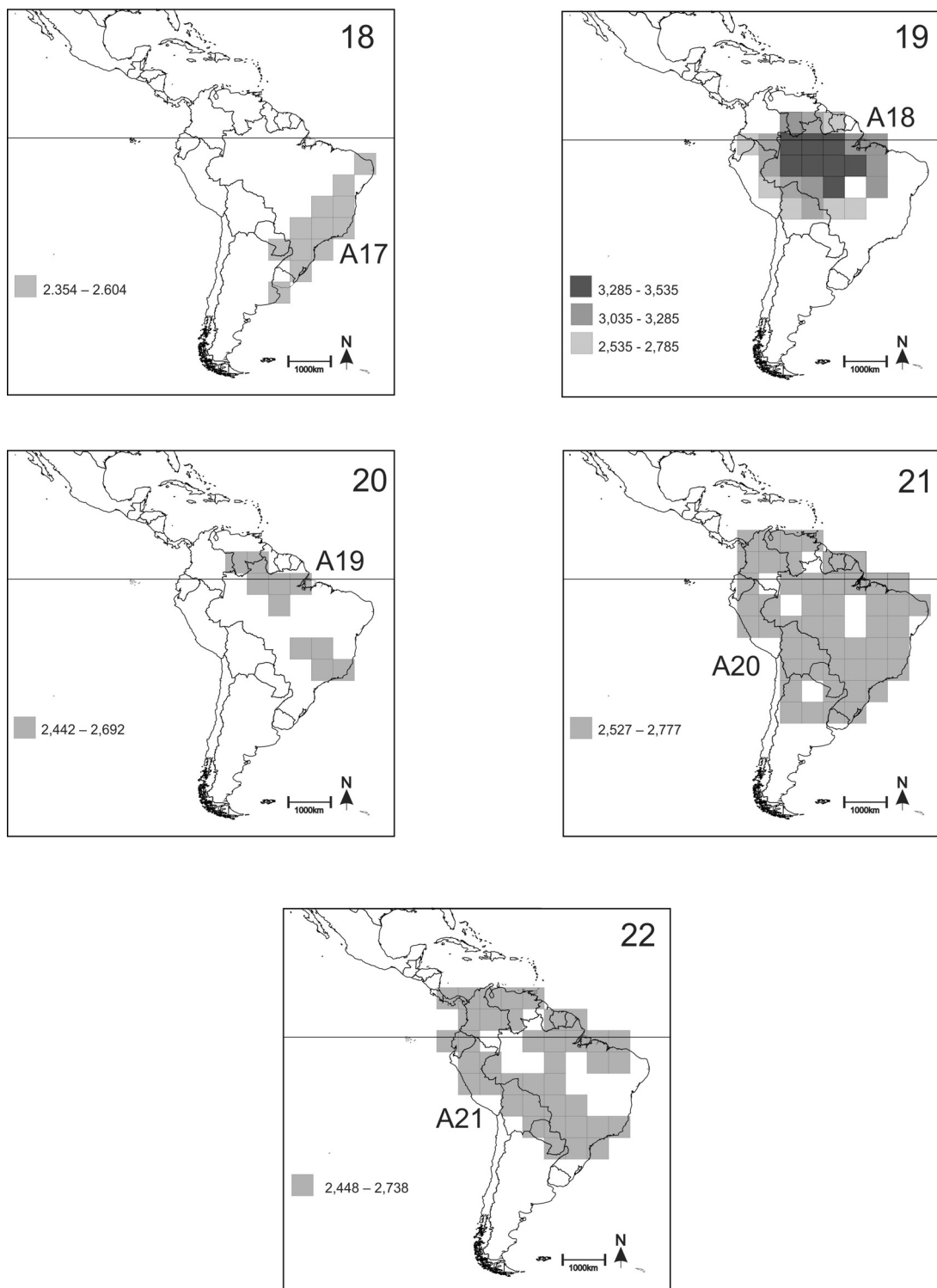
Figures 18-22. Consensus of the areas of endemism resulting from the analysis based on grid-cells of 5° latitude-longitude: 18, area 17; 19, area 18; 20, area 19; 21, area 20; 22, area 21 (for endemic taxa of the areas and respective scores of endemism, see table I).

while area 20 is southern, including portions of the Pampa and Chaco provinces.

The archipelago of Galapagos is included in a grid-cell of 5° latitude-longitude, with *Chinavia viridans* Stål, 1859, *Thyanta setigera* Ruckes, 1957 and *T. similis* Van Duzee, 1933 restricted to the area. *C. viridans* was recorded for Panama (Rolston, 1983) with no locality specified, maybe as an error. Both species of *Thyanta* was recorded only to Galapagos (Rider & Chapin, 1991).

No grouping of grid-cells (areas of endemism) was identified for the Caribbean islands, despite various species having a distribution restricted to this region: *C. euri* occurring in Mayaguana Island (archipelago of the Bahamas); *C. insulani* (Rolston, 1983) endemic to the Dominican Republic; *C. sparnia* (Dallas, 1851) endemic to Jamaica; *C. wygodzinskyi* (Rolston, 1983) occurring in the Grand Bahamas islands, Dominican Republic and British Virgin Islands ("Guana Island" and "Virgin Gorda Island"). *Chinavia* has three species occurring in the Caribbean islands and continental areas: *C. collis* (Rolston, 1983) in Cuba and in Costa Rica; *C. marginata* (Palisot de Beauvois, 1817), widely distributed in Central America, northeast of South America, Dominican Republic and Jamaica; and *C. montivaga* (Distant, 1890) with records for the Dominican Republic, Jamaica, Panama and Honduras.

DISCUSSION

Area 2 is composed predominantly by species of *Chinavia* (7 spp.), *Serdia* (7 spp.), *Antiteuchus* (3 spp.), *Agroecus* (2 spp.), *Dichelops* (2 spp.) and *Thyanta* (2 spp.). This area encompasses all of the Paraná subregion, which includes the provinces of the Brazilian Atlantic Forest, Paraná Forest and *Araucaria angustifolia* Forest, and two grid-cells in the Pampa with a lower score of endemism (Fig. 3). Area 2 is limited on the west by the Rio Paraná, where only *Serdia concolor* Ruckes, 1958 and *Dichelops avilapiresi* Grazia, 1978 cross this border. To the south of the area, only *Chinavia longicorialis* (Breddin, 1901) occurs outside of the grid-cells with a lower score. The limits of the species distribution included in area 2 are broadly congruent with the limits proposed by Morrone (2006). Based on the distribution of Peiratinae (Heteroptera: Reduviidae), Morrone & Coscarón (1996) inferred an intimate relation between the Brazilian Atlantic Forest and Paraná Forest provinces, a pattern corroborated by the data obtained here. The Rio Doce limits the northern occurrence of the species of this grouping; with the exception of *Cataulax eximius* (Stål, 1860) which has a point of occurrence on the border between Bahia and Minas Gerais, the other species do not cross the Rio Doce. Various studies infer the presence of a possible vicariant biogeographic barrier, or primary barrier to gene flow, associated with the formation of the hydrographic basin of the Rio Doce. Reference is made to this barrier in various phylogeographic studies of vertebrates, with regard to species of lizards (Gekkonidae), birds (Dendrocolaptidae) and rodents (Sigmodontinae) (Pellegrino *et al.*, 2005; Cabanne *et al.*, 2008; Ventura *et al.*, 2010) and in studies on ants (Formicidae: Ponerinae) (Mariano *et al.*, 2008).

The search by areas with grid-cells of 5° latitude-longitude allowed the identification of Panamá as an area of endemism with different scales (Figs 7, 8), which agree with Sigrist & Carvalho (2008), who associated this area with panbiogeographic nodes previously recognized by Croizat (1958). Biogeographic nodes may be interpreted as areas of great importance in the history of diversification of the taxa, and may represent the limit of ancestral biotas (Crisci *et al.*, 2003).

The portions to the west of areas 6 and 8 overlap the provinces identified by Navarro *et al.* (2007), Coastal and Andes mountain ranges, which are related and are sisters of the Guyana Shield endemic area.

The areas of endemism 9 and 10 possess three shared grid-cells due to the presence of *Thyanta xerotica* Rider, 1991 and *Serdia ruckesi* Thomas & Rolston, 1985 in both areas, but area 9 is more related to the Andean region and grouping 10 to the Amazonian region. Morrone (2004b) discussed the hybrid character of the biota of the South American transition zone, the presence of a biogeographic node in the Puna province, and the relations with Neotropical and Andean elements. Despite the relative spatial congruence of areas 9, 10 and 11, they should be interpreted as distinct areas, because of the 12 species that comprise area 11, two species are shared with area 9, two with area 10, and one with both areas, making seven species exclusive to area 11.

Area 15 differs from area 14 by including portions to the northeast of the Pampa, the south of the Puna and northern regions of the Caatinga provinces, with limits similar to those of the Neotropical region southeast component, proposed by Amorim & Pires (1996).

The Amazonian region has been traditionally treated as a historical unit, assuming that the biotic elements share a common history (see Nihei, 2008), and was identified as a single area in the area of consensus 18 (Fig. 19). However, areas of consensus 14, 15 and 16 (Figs. 15-17) demonstrate that the southeastern portion of Amazonia share elements with the Chacoan and Paraná subregions, as proposed by Nihei & Carvalho (2007) and Sigrist & Carvalho (2009). The distribution data of the taxa employed in the analysis are scarce for the Amazonian region, where they are restricted to the bank of the rivers and traditionally sampled areas. This leads to large portions of land without data of occurrence for any taxon, which could have made it impossible to define areas with greater support of endemic species. The initial groupings that gave rise to the consensus shown in area 18 vary considerably with respect to their composition of species and geographic position. The distribution data of Pentatomidae, analyzed here, did not allow us to infer with certainty if the evolution of the family in the Amazonian region corroborates a single area *sensu* Morrone (2006) or as a hybrid area (two Amazonias) *sensu* Amorim & Pires (1996).

The analyses were sensitive to the identification of areas of endemism in different scales in the Atlantic Forest (Figs. 7; 14-18), which can be related to hierarchical pattern of endemism (Espinosa-Organista *et al.*, 2001; Silva *et al.*, 2004; Sigrist & Carvalho, 2008). These groupings may indicate a possible division of the Atlantic Forest into different components of endemism.

The distribution data of the taxa studied, with different units of analysis (5° and 2.5° latitude-longitude), did not allow the identification of individual areas of endemism for the Cerrado and Caatinga provinces. Area 17 was the only area of endemism obtained, which includes the whole Caatinga province; however, the Caatinga was not identified as an isolated area of endemism in any of the analyses performed in this study. The fact of the Caatinga being part of area 17 is probably an artifact of the method used, related to the size of grid-cells employed. The methodology used in the detection of areas of endemism is especially sensitive to the lack of data in the regions studied (generally due to the missing samples), where the spatial discontinuity produced by this lack of information decreases the probability of occurrence of sympatry among the species, thereby modifying the patterns that may be encountered (Casagranda *et al.*, 2009).

Using a grouping unit based on grid-cells did not appear to be efficient in the identification of insular areas of endemism. Analytical procedures based on islands or archipelagos as grouping units may be less arbitrary than that based on grid-cells, and could allow a better exploration of distribution data for insular areas.

The areas of endemism identified here should be seen as primary biogeographic hypotheses (Morrone, 2001). The use of these areas in studies of cladistic biogeography should consider proposals based on results obtained for other taxa. Morrone (2009) proposed an approach called evolutionary biogeography, which aims to integrate methods frequently employed in different biogeographic analyses. The search for areas of endemism and for generalized tracks (resulting from panbiogeographic analyses) is defined as the first step in identifying groupings of taxa integrated in a spatial-temporal manner, called biotic components. The second step is the test of the relationships between the biotic components, based on the inclusion of the cladistic relationships of taxa and their distribution areas.

The inclusion of cladistic data in testing areas of endemism makes possible to use different units in the substitution of terminals in cladograms, which can be useful in choosing of resultant areas from analyses of endemism, as in the case of overlapping areas or with species in common (see Nihei & Carvalho, 2007). The selection of conflicting areas of endemism can be based on the congruence with the general area cladograms of the taxa analyzed. Perhaps more important than choosing areas of endemism with greater scores of endemism, would be to find areas (develop a procedure that allows choosing areas) with greater congruence with the phylogenetic data employed in biogeographic analyses, this procedure will allow (with the objective of) formulating secondary biogeographic hypotheses.

Pentatomidae distribution data has received little attention over the last decades. Despite the increasing number of works using cladistic, there is a lack of hypotheses about the distribution pattern of the group. Consistent hypotheses for Pentatomidae evolution in the Neotropical region depend on the accuracy of the units employed in the analyses, which studies of historical biogeography are represented by areas of endemism. The present study is the first to use an explicit methodology for analyzing the patterns of endemism of this family in the Neotropical region. The areas of endemism recognized here need to be refined, in order to obtain higher spatial resolution, by the inclusion of new taxa, or increase in distribution data with new samples, or even with the use of other analytical tools (*e.g.* panbiogeography).

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