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Areas of endemism in the Brazilian Atlantic Forest based on the distribution of dung beetles (Coleoptera, Scarabaeidae, Scarabaeinae)

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ABSTRACT. Our goals were to determine whether the pattern of geographical distribution of dung beetles in the Brazilian Atlantic Forest (BAF), Southeast Brazil, supports the identification of the areas of endemism in this biome, how the number and boundaries of the areas of endemism vary with the spatial scale used in the analysis, if the areas of endemism identified here are consistent with previous proposals described in the literature. We used the analysis of endemicity (NDM) on the distributional patterns of 198 species and subspecies of dung beetles in order to identify areas of endemism into grids of 0.25°x0.25°, 0.5°x0.5° and 1°x1°. A total of 15 consensus areas (CA) were identified with the different grid sizes employed (two of 0.25°, three of 0.5° and 10 of 1°). Our results support the assumptions about the influence of the grid size, since a smaller number of CA were identified for the 0.25° grids (02 CA), whereas by increasing the size of the units, there was an increase in the number of the areas of endemism (10 CA of 1°). Despite different levels of geographical congruence, the areas of endemism located in the BAF described elsewhere are corroborate, all or part of them. The overlap of these CA allowed the definition of three generalized areas of endemism: Southeast, Central and Southwest. These generalized areas encompassed habitats with great environmental variety, potentially influencing the levels of endemism of species of dung beetles. Furthermore, they were corroborated by other areas of endemism described in the literature, allowing us to argue that processes forming these regions have influenced dung beetle species as described for other groups of organisms.

KEYWORDS. Biogeography, analysis of endemicity, NDM/VNDM, consensus areas.

RESUMO. Áreas de endemismo na Mata Atlântica Brasileira baseadas na distribuição de besouros rola-bostas (Coleoptera, Scarabaeidae, Scarabaeinae). Nossos objetivos foram determinar se o padrão de distribuição geográfica de besouros rola-bostas na Mata Atlântica Brasileira (MAB), no sudeste do Brasil, permite a identificação das áreas de endemismo nesse bioma, como o número e os limites das áreas de endemismo variam com a escala espacial usada na análise, se as áreas de endemismo aqui identificadas são consistentes com propostas anteriores descritas na literatura. Utilizamos a análise de endemicidade (NDM) sobre os padrões de distribuição de 198 espécies e subespécies de besouros rola-bostas, a fim de identificar áreas de endemismo em grades de 0,25°x0,25°, 0,5°x0, 5° e 1°x1°. Foram identificadas 15 áreas de consenso (AC) com os diferentes tamanhos de quadrículas empregados (duas de 0,25°, três de 0,5° e 10 do 1°). Nossos resultados corroboram as premissas sobre a influência do tamanho da grade, uma vez que um número menor de AC foi identificado nas quadrículas de 0,25° (02 AC), enquanto que ao aumentar o tamanho das unidades, houve um aumento no número de áreas de endemismo (10 AC do 1°). Apesar de diferentes níveis de congruência geográfica, as áreas de endemismo localizadas no MAB descritas em outros trabalhos são corroboradas, total ou parcialmente. A sobreposição dessas AC permitiu a definição de três áreas generalizadas de endemismo: Sudeste, Central e Sudoeste. Essas áreas generalizadas englobaram habitats com grande variedade ambiental, influenciando potencialmente os níveis de endemismo de espécies de besouros. Além disso, eles foram corroborados por outras áreas de endemismo descritas na literatura, permitindo argumentar que os processos que formam essas regiões influenciaram as espécies de besouros como descrito para outros grupos de organismos.

PALAVRAS-CHAVE. Biogeografia, análise de endemicidade, NDM/VNDM, áreas de consenso.

An endemic area is a non-random area of congruence of geographical distribution between two or more taxa, not requiring complete agreement in limits of distributions on all possible mapping scales, but with a relatively extensive sympatry as a prerequisite (Cracraft, 1985; Platnick, 1991; Morrone, 1994). The recognition and characterization of the areas of endemism and their history can generate hypotheses about the history of the analyzed geographical units and the differentiation of clades found in them, helping to understand the biogeographical patterns and choice of priority regions for conservation (Cracraft, 1985; Costa *et al.*, 2000; Cavieres *et al.*, 2002; Sigrist & Carvalho, 2008; Aagesen *et al.*, 2013). However, the methodological difficulties related to the analysis of the areas of endemism may impose restrictions in their identification (Cracraft, 1985), especially considering that the overlap of the distributions of species is never complete, which can make the definition of an endemic area subjective (Ferrari *et al.*, 2010). The elimination of this bias results in an enhanced quantitative methodological approach, providing increased predictive power for identifying these areas (Morrone, 1994, 2009; Morrone & Crisci, 1995; Szumik *et al*., 2002; Szumik & Goloboff, 2004).

The reconstruction of evolutionary processes that contributed to diversification in the Neotropics is a challenging task due to the high species richness, the scarcity of evolutionary studies on this diversity and the severe anthropogenic pressure on their habitats, admittedly relevant characteristics of the Brazilian Atlantic Forest (BAF) (Myers *et al*., 2000; Ribeiro *et al*., 2009; Thomé *et al*., 2014). With estimates of between 8 and 16% of the remaining vegetation in South America, the BAF had an original expanse of approximately 1,400,000 km^2 in Brazil (Galindo-Leal & Câmara, 2005; Silva & Castelletti, 2005; Ribeiro *et al*., 2009). Its latitudinal variation, together with the longitudinal and altitudinal variations, contributes to the formation of highly diverse landscapes, explaining the extraordinary diversity of species in the region (Rizzini, 1997; Silva & Castelletti, 2005). Furthermore, the isolation of BAF with respect to other forest biomes in South America entails evolutionary processes forming a unique biota with numerous cases of endemism (Rizzini, 1997; Myers *et al*., 2000; Silva & Castelletti, 2005; Santos *et al*., 2007).

Dung beetles are a group of interest in conducting studies with different approaches because of the ecological functions performed by its species, such as nutrient cycling, secondary dispersal of seeds and suppression of parasites (Halffter & Favila, 1993; Nichols *et al*., 2007, 2008; Scholtz *et al*., 2009). Furthermore, the great representation of dung beetles in museums and collections, the wide geographic distribution and a strong correlation with other taxa, make this an excellent group for proposing biogeographic studies (Spector & Forsyth, 1998; Spector, 2006). The number of studies of its kind has increased in the last years in the BAF (Louzada & Lopes, 1997; Hernández, 2002; Durães *et al*., 2005; Endres *et al*., 2005; Costa *et al*., 2009; Hernández & Vaz-de-Mello, 2009; Silva & DiMare, 2012; Campos & Hernández, 2013; Culot *et al*., 2013). However, there have been no studies aimed at presenting a general proposal of biogeographic aspects of the dung beetles by identifying of the areas of endemism and the congruence of these patterns with other previously defined areas.

Accordingly, using a quantitative approach through the NDM/VNDM method (Szumik *et al*., 2002; Szumik & Goloboff, 2004), our objectives were to assess: (1) if the pattern of geographical distribution of dung beetles in the BAF supports the identification of the areas of endemism in this biome; (2) how the number and boundaries of the areas of endemism vary with the spatial scale used in the analysis; (3) if the areas of endemism identified here are consistent with previous proposals described in the literature.

MATERIALS AND METHODS

Data for distribution of the species. The analysis was carried out with 2,082 distributional records of 198 species and subspecies of dung beetles belonging to 32 genera, with taxonomic situation well resolved and existence of reliable information of geographical distribution. This represents about ¼ of the Brazilian beetle species, with all the species already described and without taxonomic problems.

The geographical coordinates of the records (Supplementary Material) were obtained and/or confirmed through various sources: the identification label of the specimens (when present in the Coleção Zoológica da Universidade Federal de Mato Grosso/Setor de Entomologia – CEMT, the standard depository for specimens collected by all current research groups working with dung beetles in the BAF and, therefore, currently the collection containing the best worldwide representation of dung beetles for this biome) or the data provided in the bibliography reviewed, some being confirmed through the website of the Brazilian Institute of Geography and Statistics – IBGE (http://www.cidades.ibge.gov.br/). When the indication of the localities did not provide the geographic coordinates, they were obtained by using the Google Earth, version 7; the GeoLoc tool, available on the website SpeciesLink (http://splink.cria.org.br/). In the absence of precise location of the registration, the seat of the municipality was used as georeferencing point.

Endemicity analysis. The definition of the areas of endemism was performed by the optimality criterion, known as endemicity analysis (EA) (Szumik *et al*., 2002; Szumik & Goloboff, 2004) using the programs NDM/VNDM, that calculates the endemicity index of a species (EIs) in accordance with the adjustment of its distribution to "random area" (sets of cells), so the higher this adjustment, the higher the score of the species (EIs varies from 0 to 1), where the endemicity index of the area (EIa) equals the sum of the EIs. Thus, an endemic area is defined by the set of cells with EIa> 2 and that have two or more endemic species.

Data were analyzed considering different sizes of grid squares to test the effect of this variable (spatial scale) in identifying of the areas of endemism (Casagranda *et al*., 2009), since areas that are not recovered with change in grid size may represent a simple artifact of this particular grid. While on the other hand, areas recovered are an important factor in the analysis of distribution patterns (Aagesen *et al*., 2009). The grid sizes employed were 0.25°x0.25°, 0.5°x0.5° and 1°x1°. The parameters used in the search for areas of endemism were area sets with scores > 2 and with two or more endemic species and 100 repetitions with 40% unique species, using the "edge proportions" option. In addition to the observed occurrences, we used three types of suppositions of occurrence (inferred, potential and assumed), since this allows sparse sampling problems to be partially resolved (for more details, see Szumik *et al*., 2002; Szumik & Goloboff, 2004; Aagesen *et al*., 2009; Casagranda *et al*., 2009). The radii of potential (R.fill) and assumed (R.ass) occurrence varied according to size of the grid (Tab. I), according to the criteria of Casagranda *et al.* (2009).

The results are presented and analyzed using consensus areas (CA), which summarize the information contained in individual areas of endemism. They were created according to the percentage of similarity of species shared between them (Aagesen *et al.*, 2013). In the present work, the flexible consensus was applied, with 40% minimum similarity of endemic species, to group areas initially identified.

Tab. I. Potential (R.fill) and assumed (R.ass) radii for identification of areas of endemism based on the distribution of dung beetles in the Brazilian Atlantic Forest.

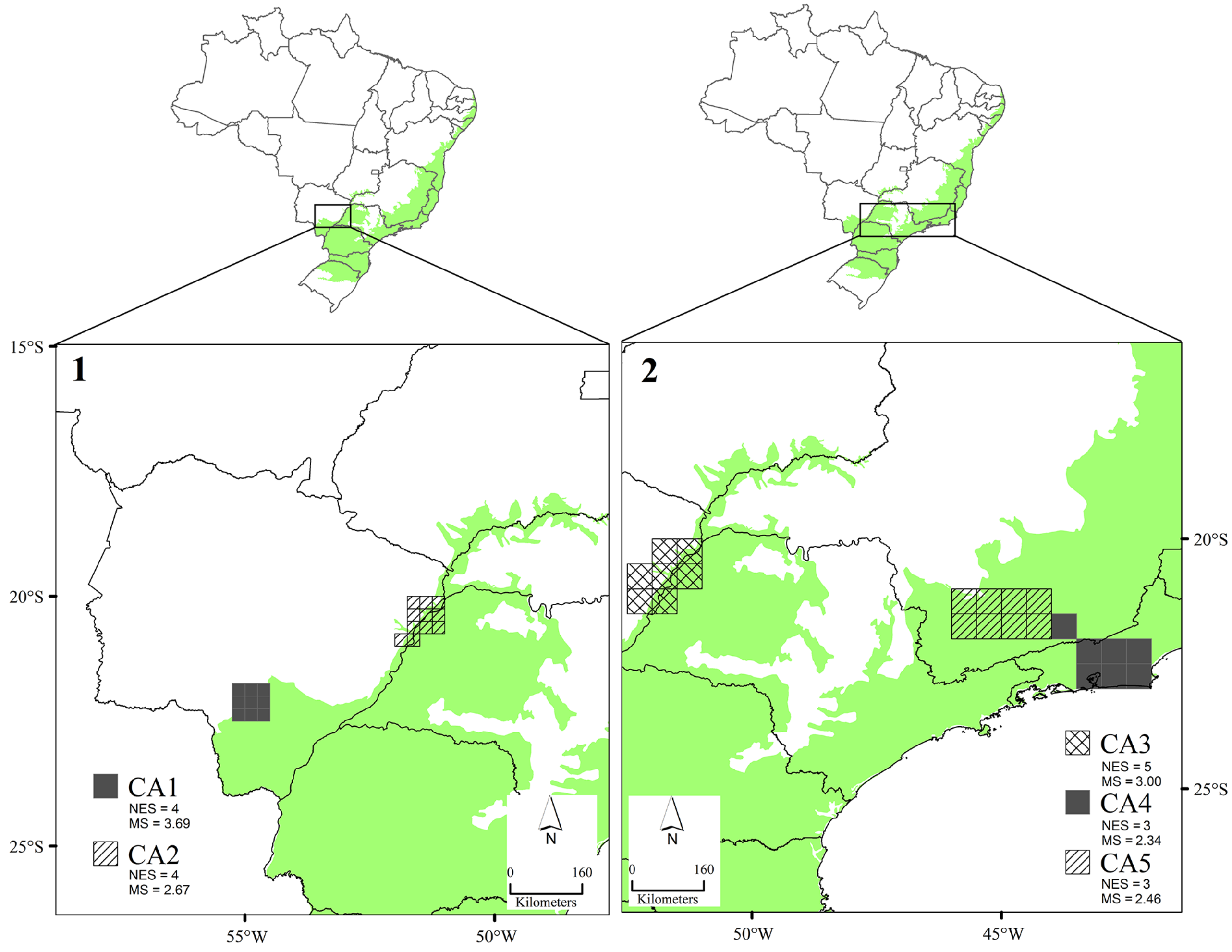
	R.fill		R.ass	
	x	y	x	y
0,25° x 0,25°	50	50	100	100
0,50° x 0,50°	20	20	50	50
1° x 1°	15	15	30	30

RESULTS

Of the 198 species, 51 (25.75%) were endemic in the grid sizes used, with 8 (4.04%), 11 (5.55%), and 45 (22.72%) species in the 0.25°, 0.5°, and 1° grid, respectively. We identified 39 areas of endemism that resulted in 15 consensus areas by employing the flexible consensus scheme. The number and location of the consensus areas by grid sizes are mentioned hereafter.

Areas of endemism. We identified two areas of endemism for the squares of 0.25° (EIa = 2.42 and 3.44), and by application of a flexible consensus, these two areas were retained (CA1 and CA2) (Tab. II). These areas are located in the western part of the BAF (bordering the Cerrado biome) (Fig. 1). Each of the CA identified showed four endemic species (Tab. II).

For 0.5° squares, four areas of endemism were identified (EIa ranging from 2.09 to 2.92). Three CA for this size squares were retained (Tab. II). We obtained a CA in the western portion of the biome, in the border region with the Cerrado (CA3; Fig. 2). The other two CA (CA4 and CA5) were located in the eastern part of BAF (Fig. 2).



Figs 1, 2. Consensus areas (CA) identified on the basis of the distribution of dung beetles in the Brazilian Atlantic Forest: 1, CA for grids of 0.25°x0.25°; 2, CA for grids of 0.5°x0.5°. NES, number of endemic species in the consensus areas; MS, maximal score of the consensus areas.

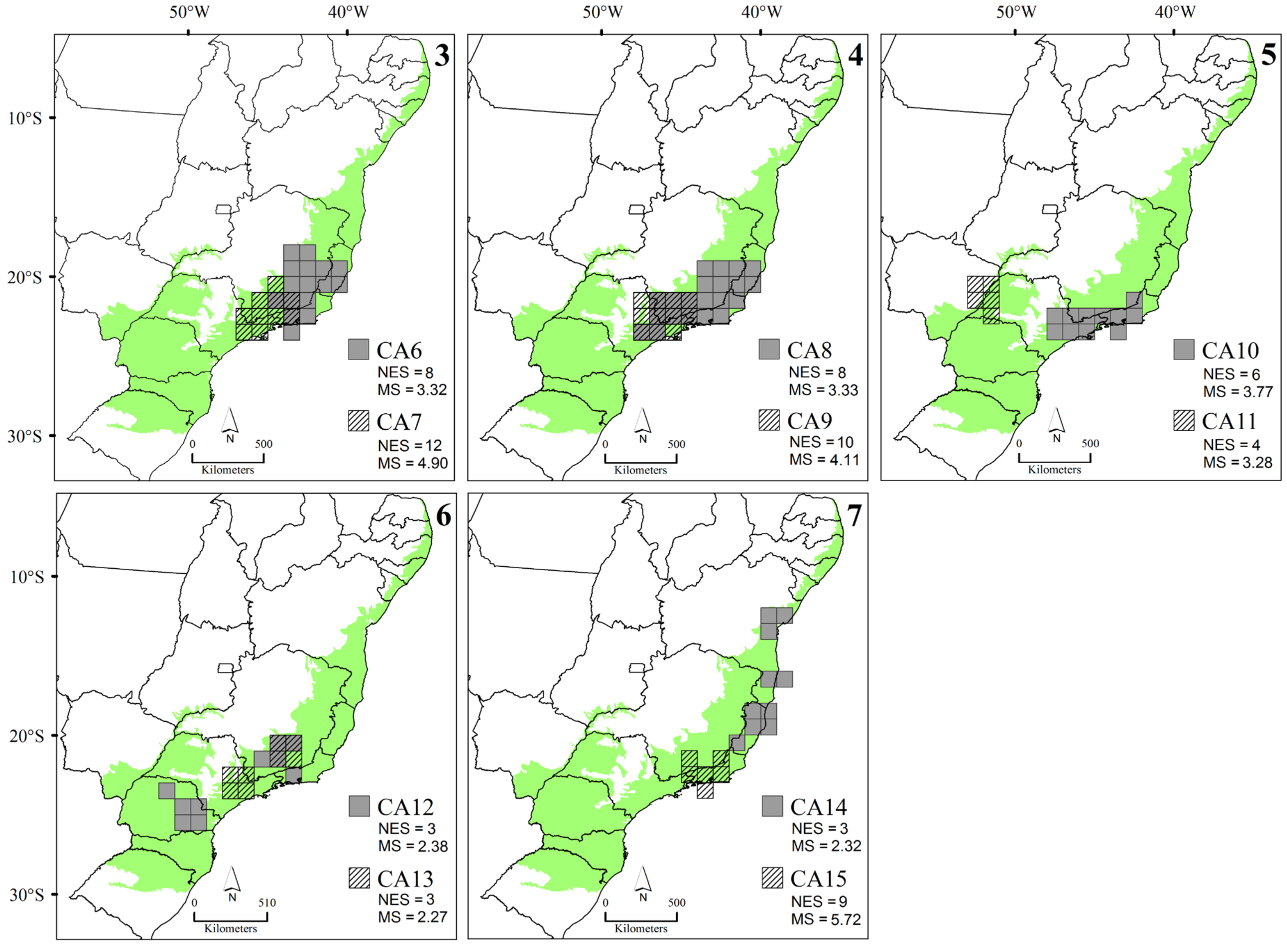
Tab. II. Defining endemic species of the consensus areas identified on the basis of the distribution of dung beetles in Brazilian Atlantic Forest (SG, size of grid; CA, number of consensus areas; MS, maximal score).

SG	CA	Endemic species (score)	MS
0.25°	1	*Canthon dives* Harold, 1868 (0.861); *Canthon laminatus* Balthasar, 1939 (0.861); *Diabroctis mirabilis* (Harold, 1877) (0.861); *Dichotomius luctuosioides* (Harold, 1869) (0.861)	3.69
0.25°	2	*Anomiopus birai* Canhedo, 2006 (0.795); *Canthon opacus* Lucas, 1857 (0.506); *Deltorhinum bilobatum* Génier, 2010 (0.795); *Dichotomius eucranioides* Pereira & D'Andretta, 1955 (0.328)	2.67
0.5°	3	*Anomiopus birai* (0.000-0.875); *Canthon fortemarginatus* Balthasar, 1839 (0.000-0.714); *Canthon opacus* (0.586-0.893); *Deltorhinum bilobatum* (0.000-0.875); *Dichotomius eucranioides* (0.586-0.893)	3.00
0.5°	4	*Anomiopus pumilius* Canhedo, 2006 (0.376); *Ontherus cephalotes* Harold, 1869 (0.857); *Ontherus insolitus* Genier, 1996 (0.857)	2.34
0.5°	5	*Canthon corpulentus* Harold, 1868 (0.750); *Canthon fallax* Harold, 1868 (0.688); *Deltochilum elevatum* (Castelnau, 1840) (0.781)	2.46
1°	6	*Anomiopus preissae* Canhedo, 2004 (0.000-0.750); *Canthon splendidus* Schmidt, 1922 (0.000-0.700); *Coprophanaeus machadoi* (Pereira & d'Andretta, 1955) (0.000-0.614); *Deltepilissus infernalis* Harold, 1881 (0.000-0.620); *Dichotomius affinis* Felsche, 1910 (0.000-0.755); *Dichotomius muticus* (Luederwaldt, 1922) (0.000-0.738); *Ontherus podiceps* Harold, 1868 (0.397-0.833); *Scatonomus chalybaeus* Erichson, 1835 (0.000-0.824)	3.32
1°	7	*Anomiopus octodentatus* Canhedo, 2004 (0.000-0.781); *Anomiopus pumilius* (0.000-0.757); *Anomiopus serranus* Canhedo, 2004 (0.000-0.336); *Anomiopus sulcaticollis* Canhedo, 2006 (0.000-0.833); *Bdelyrus bromeliatilis* Cook, 1998 (0.000-0.507); *Canthon corpulentus* (0.000-0.840); *Canthon fallax* (0.000-0.700); *Deltochilum elevatum* (0.000-0.700); *Dichotomius buqueti* Lucas, 1857 (0.000-0.625); *Ontherus amplector* Génier, 1996 (0.000-0.609); *Ontherus rectangulidens* Génier, 1996 (0.000-0.833); *Scatonomus chalybaeus* (0.000-0.231)	4.90
1°	8	*Anomiopus nigrocoeruleus* (Martínez, 1955) (0.257-0.711); *Deltochilum irroratum* (Laporte, 1840) (0.000-0.537); *Dichotomius affinis* (0.000-0.646); *Dichotomius muticus* (0.000-0.750); *Phanaeus dejeani* Harold, 1868 (0.404-0.716); *Scatonomus janssensi* Pereira, 1954 (0.000-0.681); *Silvinha unica* Vaz-de-Mello, 2008 (0.000-0.688); *Sulcophanaeus rhadamanthus* (Harold, 1875) (0.000-0.576)	3.33
1°	9	*Anomiopus serranus* (0.000-0.400); *Anomiopus sulcaticollis* (0.000-0.667); *Canthon corpulentus* (0.000-0.531); *Canthon fallax* (0.000-0.667); *Canthon muticus muticus* Harold (0.000-0.875); *Deltochilum cupreicolle* (Blanchard, 1841) (0.000-0.833); *Deltochilum elevatum* (0.000-0.667); *Deltochilum icariforme* Paulian, 1938 (0.000-0.667); *Ontherus carinicollis* Luederwaldt, 1931 (0.582-0.833); *Scatrichus bicarinatus* (Harold, 1869) (0.536-1.000)	4.11
1°	10	*Bdelyrus bromeliatilis* (0.000-0.795); *Dichotomius buqueti* (0.000-0.900); *Ontherus amplector* (0.583-0.713); *Ontherus erosus* Harold, 1875 (0.000-0.800); *Silvinha unica* (0.000-0.597); *Sulcophanaeus rhadamanthus* (0.000-0.600)	3.77
1°	11	*Canthon fortemarginatus* (0.758-0.800); *Canthon opacus* (0.758-0.800); *Dichotomius eucranioides* (0.758-0.800); *Sulcophanaeus faunus* (Fabricius, 1775) (0.636-0.758)	3.28
1°	12	*Genieridium paranense* (Arrow, 1932) (0.675); *Phanaeus dzidoi* Arnaud, 2000 (0.714); *Scatonomus thalassinus* Waterhouse, 1891 (0.750)	2.38
1°	13	*Anomiopus serranus* (0.848); *Malagoniella lanei* Lange, 1945 (0.565); *Silvinha unica* (0.614)	2.27
1°	14	*Canthon prasinus* Harold, 1867 (0.447); *Deltochilum granulosum* Paulian, 1933 (0.754); *Streblopus opatroides* Lansberge, 1874 (0.875)	2.32
1°	15	*Anomiopus pumilius* (0.589); *Deltepilissus infernalis* (0.536); *Dichotomius buqueti* (0.582); *Ontherus cephalotes* (0.708); *Ontherus insolitus* (0.667); *Ontherus rectangulidens* (0.667); *Ontherus virescens* Lucas, 1859 (0.683); *Scatonomus chalybaeus* (0.536); *Sulcophanaeus rhadamanthus* (0.509)	5.72

CA3 had five endemic species, while CA4 and CA5 each had 3 endemic species (Tab. II).

Considering the squares of 1°, 33 areas of endemism (scores ranging from 2.02 to 5.47) were identified. Flexible consensus analysis identified 10 CA (Tab. II). Thus, considering the largest portion of each of these areas, we have the CA6, CA7, CA8, CA9, CA10, CA12, CA13 and CA15 had a great amount of overlap between their geographical units, where they were located in the eastern part of the BAF (Figs 3-7). CA11 was located in the western region of the biome, bordering the Cerrado biome (Fig. 5). CA14 was the only one that encompassed the northernmost stretches of the BAF (Fig. 7).

Geographical overlap between consensus areas. Comparing the boundaries and the geographic location between areas, CA1 showed no overlap with any area identified by other size grids, unlike CA2, which had its limits completely encompassed by CA3 and CA11 (Fig. 8). This geographical overlap indicates a hierarchical pattern in the composition of the endemic species, since all the species in CA2 are also endemic in CA3, and most of the species in CA3 are endemic in CA11 (Tab. II). On the other hand, the CA of 0.5° grids showed their limits completely encompassed by at least one of the areas identified by 1° grids, for both the eastern and western portions of BAF (Fig. 8). The level of overlap between CA of the 1° squares was extensive, considering that most of these areas were located in the eastern portion of BAF, except CA11 (western), with no overlap with other areas for that size and CA14 (northern), with a partial overlap with CA6 and CA8 (Figs 3-7, 8). This



Figs 3-7. Consensus areas (CA) for grids of 1°x1° identified on the basis of distribution of dung beetles in the Brazilian Atlantic Forest. NES, number of endemic species in the consensus areas; MS, maximal score of the consensus areas.

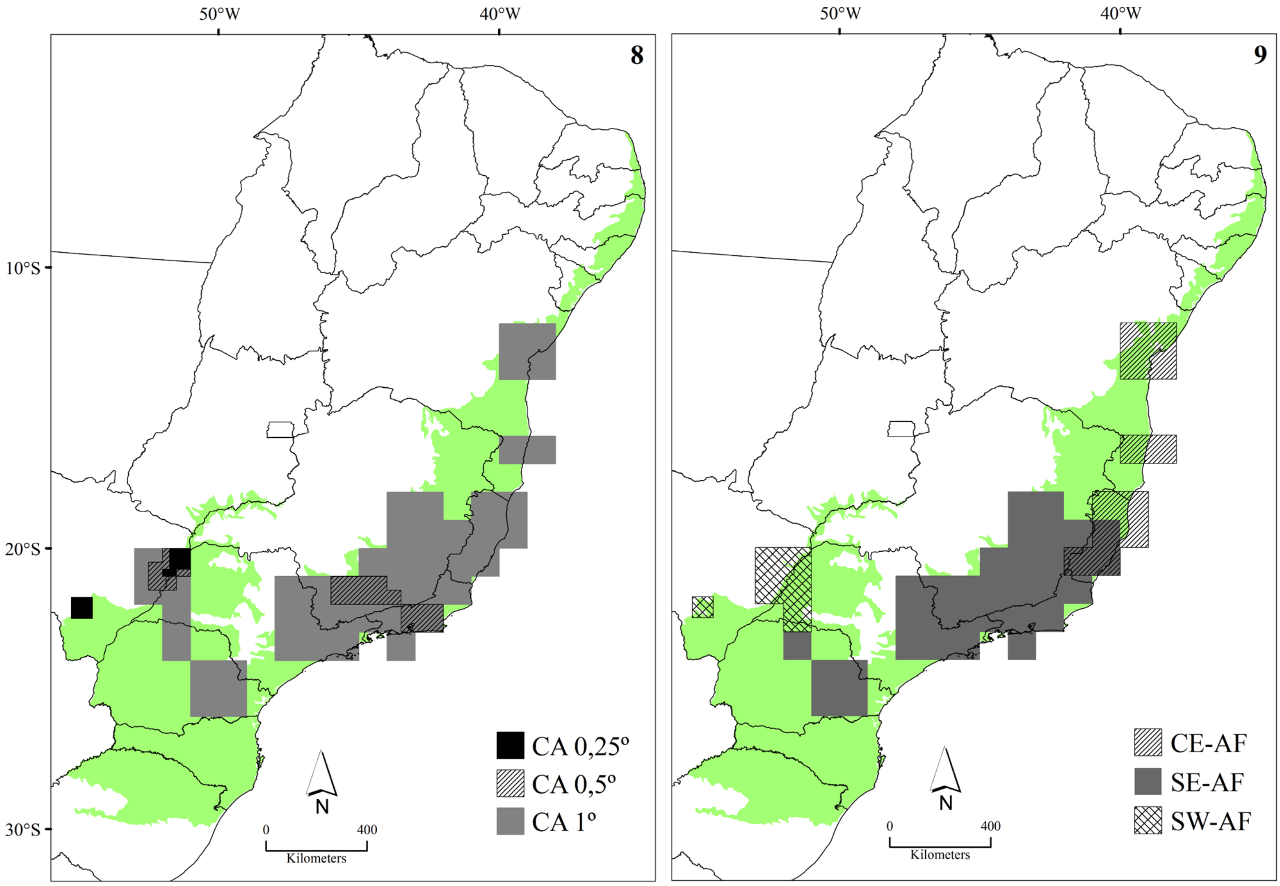
region provides more information about the distribution of the dung beetles, thus reducing sample gaps and generating concordant distribution patterns. This results in more areas of endemism and higher scores in these areas.

The level of geographical overlap of the CA was the criteria used to define three generalized areas of endemism: Southeast Atlantic Forest (SE-AF), Central Atlantic Forest (CE-AF) and Southwest Atlantic Forest (SW-AF). This procedure was adopted as a descriptive tool of the data because this overlap suggested that these regions exhibited a high degree of endemicity, with the occurrence of taxa restricted to each region, but shared between the CA that formed them (the same procedure was adopted by Prado *et al*., 2015). The northern and southern regions not encompass any CA, preventing the definition of generalized areas of endemism in these stretches of the BAF.

Southeast Atlantic Forest (SE-AF; Fig. 9). This region proved important because of the number of CA identified, comprises two CA of 0.5° grids (CA4 and CA5) and 08 for the 1° grids (CAs 6, 7, 8, 9, 10, 12, 13 and 15), located primarily within the states of Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo, with the exception of CA12 which is formed by two disjunct groups of squares, one of which was located in the state of Paraná (Figs 2, 3-7, 9). The highest scores were obtained, all with 1° squares (Tab. II). Of the 38 endemic species, six of them – *Anomiopus pumilius* Canhedo, 2006; *Canthon corpulentus* Harold, 1868; *Canthon fallax* Harold, 1868; *Deltochilum elevatum* Castelnau, 1840; *Ontherus cephalotes* Harold, 1869; *Ontherus insolitus* Génier, 1996 – are endemics of the CA in the two grid sizes (0.5° and 1°), the other species were found only in CA of 1º grids (Tab. II).

Central Atlantic Forest (CE-AF; Fig. 9). It is formed by one endemic area of 1° squares (CA14), covering of Espírito Santo State and the coastal region of southern and central Bahia (Figs 7, 9), with two of the lowest scores of endemism with respect to other CA identified (Tab. II). Only three species were endemic – *Canthon prasinus* Harold, 1867; *Deltochilum granulosum* Paulian, 1933; *Streblopus opatroides* Lansberge, 1874 (Tab. II).

Southwest Atlantic Forest (SW-AF; Fig. 9). This region included four CA in all grid sizes used (CA1, CA2, CA3 and CA11). One of the 0.25° areas was located in the southern portion of Mato Grosso do Sul State and the other on the border of this state with São Paulo State. The 0.5° and 1° areas were located between the states of São Paulo



Figs 8, 9: 8, Geographical overlap of the consensus areas, in the three grid sizes, identified on the basis of distribution of dung beetles in the Brazilian Atlantic Forest; 9, generalized areas of endemism defined on the basis of the localization and overlap of the consensus areas identified (SE-AF, Southeast Atlantic Forest; SW-AF, Southwest Atlantic Forest; CE-AF, Central Atlantic Forest).

and Mato Grosso do Sul, fully overlapping each other and one of the 0.25° areas (Figs 1, 2, 5, 9). The scores of these CA were intermediate in relation to other areas identified (Tab. II). Of the ten species in this region, only *Canthon opacus* Lucas, 1857 and *Dichotomius eucranioides* Pereira & D'Andretta, 1955 were found in all the grid sizes used in the analysis, where the rest were restricted to two or only one of the sizes (Tab. II).

DISCUSSION

Spatial scale. Although there are objective operational units, the use of grids can influence the results, showing different patterns of endemicity according to the grid size used in the analysis (Szumik *et al*., 2002; Szumik & Goloboff, 2004; Casagranda *et al*., 2009). The use of very small grids leads to an extremely discontinuous distribution, making areas of endemism difficult to identify or very small. On the other hand, very large grids recognize areas of endemism that are very extensive and have many endemic species (Szumik *et al*., 2002). Thus, the use of multiple grid sizes serves as a supporting measure for the areas of endemism identified (Aagesen *et al*., 2009; Casagranda *et al*., 2009), showing patterns which vary both in shape and in size (Szumik *et al*., 2012).

Our results support these assumptions, since a smaller number of CA were identified for the 0.25° grids (02 CA), whereas by increasing the size of the units, there was an increase in the number of the areas of endemism (10 CA of 1). Smaller numbers of endemic species were found with the smaller size grids (except CA14), reinforcing the sensitivity of the discontinuity analysis of the data generated by the use of small grids (Casagranda *et al*., 2009). The number of endemic species of the CA14 (forming the CE-AF) can be explained by the lack or heterogeneity of the distribution of occurrence records of taxa, reducing the possibility of sympatry between species, required to define areas of endemism (Casagranda *et al*., 2009; Szumik *et al*., 2012), also justifying the lack of areas of endemism in the northern and southern regions of the BAF. Our results support the assumption that the use of various grid sizes increase the chances of finding patterns of endemism that would not be revealed by a single spatial scale (Prado *et al*., 2015). In the BAF, there are environments that vary in altitude as well as longitudinally and latitudinally, which can result in patterns of endemism at different scales.

Areas of endemism in Brazilian Atlantic Forest: comparison with other studies. Although we found areas of endemism with different levels of geographical congruence, the areas of endemism located in the BAF described elsewhere are corroborate, all or part of them (Cracraft, 1985 - birds; Amorim & Pires, 1996 - flies and primates; Costa *et al*., 2000 - mammals; Silva *et al*., 2004, 2012 - birds and vertebrates, respectively; Silva & Castelletti, 2005 - birds, primates and butterflies; Sigrist & Carvalho, 2008 - arthropods, plants, reptiles and amphibians; Löwenberg-Neto & Carvalho, 2009 - flies; DaSilva & Pinto-da-Rocha, 2010 - harvestmen; Ferrari *et al*., 2010 - true bugs). Still, considering the level of geographic congruence of the consensus areas, three different groups of generalized areas of endemism latitudinally and longitudinally arranged were defined in the BAF.

The first was SE-AF, formed by a large number of congruent CA. Sigrist & Carvalho (2008), in analyzing the distribution of different organisms, identified areas of endemism that showed similar geographical localization as the SE-AF, i.e., between Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo states. Cracraft (1985) studied the distribution of birds in South America and identified two areas of endemism in a region encompassed by the BAF. One of these was called Serra do Mar, comprising a narrow coastal strip from Pernambuco to Santa Catarina states. However, this author warned of the possible subdivision of this center of endemism with increasing distribution information of species, proven not only for birds (Silva *et al*., 2004), but also for other organisms, including primates, butterflies and birds (Silva & Castelletti, 2005) and harvestmen (DaSilva & Pinto-da-Rocha, 2010). Comparing the SE-AF with these cited works, it is evident that there is a great distinction in the boundaries of the areas of endemism, because most of them encompass coastal parts of this region. The SE-AF group, however, extends to more inland regions bordering the Cerrado, encompassing areas of endemism of different sizes cited in the literature, such as the areas São Paulo-Rio de Janeiro (SPRJ), northern Rio de Janeiro (NRJ) and parts of southern Bahia (SBA) and Minas Gerais and Bahia (MGBA) identified by Amorim & Pires (1996) and also five areas of the central block described by DaSilva & Pinto-da-Rocha (2010). Some broader areas, described in the literature as defining of different endemic regions, coincided with the SE-AF, such as the Serra do Mar and Interior Forest presented by Silva & Casteleti (2005); and Paulista and SE coast described by Costa *et al*. (2000). In addition, the analysis employed by Löwenberg-Neto & Carvalho (2009) identified areas of endemism located in the portion of southern BAF, with a geographic location consistent with SE-AF.

The second group, CE-AF, was formed by one CA of 1° cells, with a high level of congruence with previous descriptions. This area has geographic similarity with the endemic area Bahia, described by Silva & Casteleti (2005), although these authors described a large continuous area stretching from Sergipe to Espírito Santo states. DaSilva & Pinto-da-Rocha (2010) identified two separate areas of endemism, both encompassed by CE-AF, one in Espírito Santo and the other in southern Bahia, with the latter being partially consistent with one of the areas described by Sigrist & Carvalho (2008). Besides these, Silva *et al*. (2004) analyzed the geographical distribution of birds and also found an endemic area called Coastal Bahia, between the central and southern part of that state, confirming the importance of this coastal region in terms of endemism.

The third group, SW-AF, was established by the identification of consistent CA in the three grid sizes used, characterized by the smallest amount of information that support comparisons with other areas of endemism described in the literature. In most studies, this region is situated in areas of broader endemism, which include the southeastern and southern parts of the BAF (Costa *et al*., 2000; Silva & Casteleti, 2005; Sigrist & Carvalho, 2008). According to the representation of endemism by Silva *et al*. (2012), this area is in what was called the SW1 component (component southwest 1) defined on the basis of areas of endemism identified in the studies referred to by these authors. Two of these works, of Carnaval & Moritz (2008) and Carnaval *et al*. (2009), defined this region as having favorable climatic stability for the maintenance of the biome, even with the Pleistocene climatic variations.

Considering the regionalization described by Morrone (2014), the BAF (in the Chaquenha sub-region - Paraná Domain) encompasses three different provinces: Atlantic, Paraná Forest and Araucaria Forest, occupying latitudinally arranged narrow strips along eastern Brazil, aside from the Araucaria Forest, located in the southern region. On the basis of our results, most of the CA were spatially coincident with more than one of these provinces, a result also corroborated by Löwenberg-Neto & Carvalho (2009) in a continental analysis. Exceptions to this pattern would be the CA4 (coinciding with the Atlantic province) and CA5 (coinciding with the Paraná Forest province), probably due to the intermediate grid size, reinforcing the idea that some biogeographic patterns can be better demonstrated if various sizes of geographical study units are used (Casagranda *et al*., 2009). Since the lack of complete congruence between the geographic limits of our areas of endemism and biogeographical provinces proposed by Morrone (2014), we can infer a strong relationship between them, as it was already found for species of Heteroptera of the Atlantic and Paraná Forest provinces (Morrone & Coscaron, 1996; Ferrari *et al*., 2010). This was pointed out by the CA12, which is represented by the disjunction of two sets of cells, one to the north, between the Atlantic and Paraná Forest provinces, and the other to the south, located on the Araucaria Forest province. In addition, Löwenberg-Neto & Carvalho (2009) recognized an extensive diversification area (for species of Muscidae), which would cover the SE-AF and CE-AF.

Although there are regions with substantial importance, considering the studies that define areas of endemism within their boundaries (Amorim & Pires, 1996; Costa *et al*., 2000; Silva & Casteleti, 2005; Sigrist &

Carvalho, 2008; DaSilva & Pinto-da-Rocha, 2010; Silva *et al*., 2012; Prado *et al*., 2014), the extreme north and south of the BAF did not include exclusive CA identified on the basis of the distribution of dung beetles, despite they are widely distributed in these regions. However, we are aware of several new (undescribed) species from those regions that may be responsible for this scenario to change in the future, considering taxonomic revisions on the way and future ones (FZVM, pers. comm.).

Historical processes and the generalized areas of endemism in the Brazilian Atlantic Forest. The relictual nature of the distributions of some taxa of dung beetles has been described and eventually related to climatic variations of the Pleistocene, such as for *Coprophanaeus bellicosus* (Olivier, 1789) (Silva, 2011), *Phanaeus* Macleay (*splendidulus* group, which includes the species *P. dejeani* Harold, 1868, endemic to CA8) (Edmonds, 1994); or two species of *Bdelyrus* Harold present in the BAF and included in our analyses (*B. braziliensis* Cook, 1998 and *B. bromeliatilis* Cook, 1998, the latter considered endemic to CA7 e CA10). These variations strongly influenced the environmental conditions in the tropics, changing the distribution of forest and non-forest environments, thanks to fluctuations between wet and dry climates (Haffer, 1969). The inferences regarding habitat fragmentation in the BAF by paleo-ecological models have demonstrated a reduction in forest environments and increase in open landscapes, where such models even provided assumptions about the location of these forest refuges (Carnaval & Moritz, 2008). These predictions establish that the Pleistocene climatic variations created stable areas (refuges) in northern BAF, while in the south, the severe forest contractions almost eliminated this biome and the species dependent on it. Thus, we hypothesized that variation in the distribution of forest and non-forest environments because climatic oscillations caused the greater adaptive success in exploiting more specific niches for species of dung beetles. Thus, it would necessary to widen faunistic survey methods so that they can sampled those species with different habits, as described for species associated with latrines or nests of mammals (Arias-Buriticá & Vaz-de-Mello, 2012), accumulated debris in the water deposition spaces between leaves of terrestrial and arboreal bromeliads (Cook, 1998), social insect nests (Génier, 1996; Edmonds, 2000), fungi (Edmonds, 2000) or terrestrial snails (Vaz-de-Mello, 2007).

Rivers and mountains are often associated with the distribution boundaries of species in the BAF (Amorim & Pires, 1996; Costa *et al*., 2000; Sigrist & Carvalho, 2008; DaSilva & Pinto-da-Rocha, 2010; Thomé *et al*., 2014). Among the rivers, the Paraíba do Sul (Amorim & Pires, 1996; Sigrist & Carvalho, 2008), São Francisco (Carnaval & Moritz, 2008; Silva *et al*., 2012) and Doce (Pellegrino *et al*., 2005; Thomé *et al*., 2014) are cited as the most important in the definition of high diversity and endemism in the BAF. The course of the Rio Doce was consisting with the boundaries between the CE-AF and SE-AF. Ferrari *et al*. (2010) also raised the possibility of the role of the Rio Doce in the formation of the areas of endemism, but pointed out that this barrier did not apply to all species of Heteroptera analyzed. This partial impairment in the occurrence of the species was also evidenced by our analysis, since one of the defining species of CE-AF (*Canthon prasinus*) occurred south of the Rio Doce.

Mountain ranges also represent an important factor in the distribution of dung beetles, whether because of the adaptive capacity of their species at high altitudes (Edmonds, 1994; Canhedo, 2006), or the separation of fauna of distinct biogeographic units (Lobo & Halffter, 2000; Escobar *et al*., 2005, 2006), even on restricted spatial scales (Daniel *et al*., 2014). The SE-AF encompassed a great altitudinal variety, since the main mountains of BAF are within its boundaries, such as the Serra do Mar and Mantiqueira, recognized for their importance in defining areas of high diversity and endemism (Amorim & Pires, 1996; Costa *et al*., 2000; Sigrist & Carvalho, 2008; Löwenberg-Neto & Carvalho, 2009; DaSilva & Pinto-da-Rocha, 2010; Thomé *et al*., 2014). The occurrence of endemic species of *Ontherus* Erichson, 1847 that belong to different monophyletic groups of the subgenus *Ontherus* s. str. - *O. amplector* Genier, 1996; *O. carinicollis* Luederwaldt, 1931; *O. cephalotes*; *O. erosus* Harold, 1875; *O. insolitus*; *O. podiceps* Harold, 1868; *O. rectangulidens* Génier, 1996 and *O. virescens* Lucas, 1859 (Génier, 1996) - define some CA of SE-AF. This therefore allows us to infer that the particularities of this region would be responsible for adaptive radiation events and speciation, especially considering that most species of this subgenus is restricted to altitudes below 1000 meters above sea level, resulting in the variation in altitudinal gradient of this area and fostering the separation and differentiation of species from common ancestors.

In this study, we recognize the possibility that there are many factors potentially able to shape the distribution of species of the BAF and other biomes and to influence the relationships between them (Costa, 2003), including the intrinsic attributes of different species, such as responses to the same environmental or geologic characteristics or different response times of species isolated by the same barrier (Zink *et al*., 2001). However, on the basis of the cited references, we hypothesize that these vicariant factors influenced the formation of the generalized areas of endemism identified herein, although our analyses are not supported by temporal or phylogenetic data.

Finally, we advise caution in the range of conclusions and extrapolations made on the basis of our results, since a clear and objective definition of the areas of endemism and its potential as a guiding factor for conservation measures advances through the increase in studies with dung beetles, whether through the inventory of fauna - allowing a better understanding of the distributions of species - or through taxonomic revisions - because of the high capacity to change, sometimes dramatically, the distribution pattern of revised species.

Supplementary material. The following online material is available for this article: The geographical coordinates of the records.

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