ORIGINAL ARTICLE

Species richness and areas of endemism of oryzomyine rodents (Cricetidae, Sigmodontinae) in South America: an NDM/VNDM approach

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ABSTRACT

Aim To infer areas of endemism for the tribe Oryzomyini in South America by employing a database of species richness and geographical distribution, and to compare these results with areas of endemism and species richness proposed in the literature for other taxa.

Location We analysed specimens of the tribe Oryzomyini distributed throughout South and Central America, which are housed in European, North and South American museums and collections.

Methods We analysed 2768 occurrence records for 102 species of the tribe Oryzomyini using the NDM/VNDM algorithm and three different grid sizes to assess the possible effects of grid cell area on the results.

Results Using the overlap of consensus areas in South America, we identified three generalized areas of endemism for the Oryzomyini: north-western South America (NWSA), eastern South American (ESA), and northern South America (NSA); we also identified the Galápagos archipelago (GA) as an area of endemism.

Main conclusions Areas of endemism detected in the continental portion of South America include its three main mountain chains: the Andes Cordillera, the Guyanan Shields, and an area east of the Brazilian Shield named Serra do Mar. Each of these regions encompasses many different types of vegetation, and the species richness and composition of the areas of endemism of the tribe are directly related to this environmental diversity. Different grid sizes affected the distributional heterogeneity of the consensus areas. The smallest grid cell size identified mainly Andean areas, which contain a higher number of more exclusive species in a small area along a steep elevational gradient. In contrast, the largest grid size identified areas of endemism along an environmental gradient that co-varied with latitude and longitude. The identified areas of endemism are corroborated by previous studies on other taxa.

Keywords
Andes, biogeography, Brazilian Shield, distribution, forest areas, Galápagos archipelago, Guyanan Shield, Neotropical rodents, open areas, transitional areas.

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INTRODUCTION

Patterns of geographical distribution and biological diversity provide fundamental information for the detection of areas of endemism, which are important elements in biogeographical studies (Morrone, 1994). Traditionally, such patterns have been considered testimony of historical events that affected many taxa simultaneously (Müller, 1973; Cracraft, 1985), and, as such, these centres unite the distribution of unique species assemblages that should be prioritized in conservation

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programmes (Carvalho, 2011). There have been several efforts in recent decades to define the concept of area of endemism (see Parenti & Ebach, 2009 for a review), to identify centres of endemism for many living taxa in South America (e.g. Müller, 1973; Cracraft, 1985; Sigrist & Carvalho, 2008; Szumik *et al.*, 2012; Escalante *et al.*, 2013a,b, 2014), and to develop and enhance theoretical concepts and methodologies to standardize these searches (e.g. Platnick, 1991; Morrone, 1994, 2001; Szumik *et al.*, 2002; Szumik & Goloboff, 2004; Porzecanski & Cracraft, 2005; Parenti & Ebach, 2009).

Patterns of richness of rodents in South America, a diverse assemblage comprising approximately 642 species (Patton *et al.*, in press), have been discussed elsewhere (Hershkovitz, 1969; Reig, 1986; Amori *et al.*, 2013). However, there have been few studies on the distribution, species richness, and patterns of endemism of the tribe Oryzomyini (Sigmodontinae), the most species-rich group of cricetid rodents with 130 species (Prado & Percequillo, 2013) and the most geographically widespread, occurring throughout South and Central America and marginally distributed in southern North America. The taxonomy, geographical distribution and phylogenetic relationships of this group have been studied in recent decades, especially in South America (e.g. Weksler *et al.*, 2006; Percequillo *et al.*, 2011; Pine *et al.*, 2012; Prado & Percequillo, 2013), but an understanding of the biogeography of the tribe Oryzomyini remains in its infancy (Reig, 1986; Weksler *et al.*, 2006; Valencia-Pacheco *et al.*, 2011; Prado & Percequillo, 2013).

Previous hypotheses on the areas of endemism for the order Rodentia, or even for the subfamily Sigmodontinae or tribe Oryzomyini, are lacking for South America. Former studies, focusing on species richness and patterns of distribution employing restricted databases (Reig, 1986), range maps (Amori *et al.*, 2013) or more detailed databases (Prado & Percequillo, 2013), advocated that the northern Andes exhibits the largest diversity of the tribe Oryzomyini (Reig, 1986), that western margins of the Amazon Basin, Guyanan Shield and Brazilian Shield represent areas of great richness for the order Rodentia (Amori *et al.*, 2013), and that the Andean Cordillera, the Amazon forest and the Brazilian Atlantic Forest exhibit high generic and specific diversity for the tribe (Prado & Percequillo, 2013).

Employing the database of Prado & Percequillo (2013) and using a quantitative approach, the NDM/VNDM method (Szumik *et al.*, 2002; Szumik & Goloboff, 2004), our aims were to evaluate: (1) whether species richness and the geographical distribution of the tribe Oryzomyini in South and Central America support the inference of consistent areas of endemism in South America, employing different grid sizes; and (2) whether such areas of endemism are congruent with previous areas of endemism (e.g. Müller, 1973; Cracraft, 1985) and regions of greater species richness and diversity (Reig, 1986; Amori *et al.*, 2013; Prado & Percequillo, 2013) in South America, and are also in accordance with the evolutionary history of the tribe (Percequillo *et al.*, 2011; Pine *et al.*, 2012; Machado *et al.*, 2013; Parada *et al.*, 2013).

MATERIALS AND METHODS

In order to identify areas of endemism of the oryzomyine rodents in Central and South America, we employed a database containing 2768 records for 102 species from approximately 2170 collection localities that were obtained by direct examination of nearly 5000 specimens housed at several European, North and South American museums. For some genera we employed additional data from the literature: for *Holochilus* we used data from Hershkovitz (1955) and Voglino *et al.* (2004); for *Oecomys* we used data from Patton *et al.* (2000), Voss *et al.* (2001), Rocha *et al.* (2011) and Hice & Velazco (2012); for *Oligoryzomys* we used information available in Myers & Carleton (1981), Myers *et al.* (1995), Patton *et al.* (2000), Andrades-Miranda *et al.* (2001), Voss *et al.* (2001), Palma *et al.* (2005), Weksler & Bonvicino (2005) and Paresque (2010); and for *Tanyuromys* we consulted Pine *et al.* (2012). A list of institutions, complete geographical information regarding the specimen collection sites, distribution maps, and species authorities for oryzomyine species can be found in Prado & Percequillo (2013).

There are gaps in the geographical coverage (see Fig. 51 in Prado & Percequillo, 2013), and some gaps represent real absences (e.g. in Patagonia and the Atacama Desert), while others represent sampling artefacts (e.g. the lack of samples from some areas in Amazonia). Nonetheless, this database meets the criteria of quality of biodiversity databases discussed by Hortal *et al.* (2007), given that we personally identified (taxonomic accuracy) and assembled information on collection localities (geographical accuracy) of specimens from all available collection localities within the studied collections, covering most of the known geographical distribution of the oryzomyine genera (exhaustiveness).

NDM has recently been used to study highly diversified datasets that are composed of hundreds of taxa from higher taxonomic categories from continental (Escalante *et al.*, 2007, 2010), insular (Carine *et al.*, 2009) and local (Szumik *et al.*, 2012) perspectives. Here we apply this methodology to a more taxonomically restricted monophyletic lineage, a tribe with tens of closely related taxa, and a continental-scale distribution. Although the employment of a monophyletic lineage could bias the analysis, because the identification of areas of endemism should employ multiple groups of organisms (see Parenti & Ebach, 2009), it is relevant to notice that the currently established four clades of the tribe, A, B, C and D (Pine *et al.*, 2012), experienced distinct evolutionary trajectories in space and probably in time (Weksler, 2006). Therefore, we are confident that sympatric members of the different four clades experienced similar ecological and historical events, and that using them does not violate the principle of reciprocal illumination (Hennig, 1966), the search for patterns or explanatory hypothesis employing different types of evidence, either fields of knowledge or taxonomic groups.

Delimitation of areas of endemism

The dataset was analysed using the heuristic algorithm of NDM/VNDM, version 2.7, developed by Goloboff (2001), Szumik et al. (2002) and complemented by Szumik & Goloboff (2004). This analysis is used to determine areas of endemism based on an optimality criterion, taking into account the position of taxa in space as a component of the analysis (Szumik et al., 2002); this method also considers spatial information in the delimitation of areas and permits overlap between areas of endemism. The algorithm searches for areas of endemism by evaluating the spatial concordance regarding the presence of two or more taxa for a given set of cells (area of endemism) and calculates a score of endemicity for a given taxon according to how its distribution corresponds to a particular set of cells (Szumik et al., 2002).

Distribution maps were constructed with latitude and longitude grid sizes of 2.0°, 3.0° and 4.0°. These grid sizes were chosen based on the recommendations of Aagesen et al. (2009) and Escalante et al. (2010, 2013a). The use of three different grid sizes enabled us to examine the effect of this parameter on inferred patterns of richness/endemism. The analyses were conducted by saving temporary sets within 0.99 of the current score; in sets that had two or more endemic species, scores above 2.0 were saved. Cells were swapped one cell at a time. Subsets were considered overlapping if 50% of the species were unique, and the search was repeated 100 times. We selected species with a minimum score of 0.4 (Escalante et al., 2013a) and we computed the consensus areas of endemism using a cut-off of 100% similarity in species, and the strict consensus (Szumik et al., 2002).

To generate maps of the areas of endemism, we first converted the three different outputs of each grid size obtained using the NDM/VNDM software (TXT format) into shape files (SHP format) employing DIVAGIS (Hijmans et al., 2001). We plotted these grid shape files together using the software ARCGIS 9.3 (ESRI, Redlands, CA, USA).

RESULTS

The analysis employing the 2.0° grid identified only three areas of endemism. The consensus analysis necessarily produced the same result in this case, because the areas are contiguous and non-overlapping; these areas are associated with the Andean Cordillera and Galápagos archipelago (Table 1, Fig. 1). The search using the 3.0° grid identified eight areas of endemism and seven consensus areas, mainly associated with the central and northern Andes, eastern South America, and the Guyanan Shield (Table 1, Fig. 2). Finally, the analysis with the 4.0° grid size yielded 22 areas of endemism, and the consensus analysis resulted in 20 areas, which cover most of the South American continent (except for the central Brazilian Amazonia and Cerrado as well as the southern Cone) and Central America (Table 1, Fig. 3).

Thus, the overlapping patterns of the aforementioned areas of endemism (Fig. 4) allowed the recognition of three generalized areas of endemism on the continent for the tribe Oryzomyini, named: (1) north-western South America (NWSA), which included areas 1, 2, 4–8, 11, 12, 14–23, 25, 26 and 30; (2) eastern South America (ESA), which comprised areas 9, 13, 27 and 29; and (3) northern South America (NSA), which is formed by areas 10 and 24. In addition to these three major continental areas, an insular one, (4) the Galápagos archipelago (GA), was recovered in two grid sizes and included areas 3 (obtained in the 2.0° approach) and 28 (the same area obtained in the 4.0° approach). We selected these four areas as main areas of endemism, because the overlap and proximity of several consensus areas obtained with different grid sizes suggest consistent evidence that these regions exhibit a high degree of endemicity, with the presence of restricted and shared taxa.

North-western South America (NWSA)

This area includes consensus areas that were detected by all grid sizes using NDM/VNDM (Figs 1–3), and the number of consensus areas found for each grid and their scores are listed in Table 1. Three montane species (Nephelomys childi, N. pectoralis and Oreoryzomys balneator) and two lowland cis-Andean species (Scolomys melanops and Zygodontomys brunneus) provide support of the consensus areas for the three grid sizes (areas 1, 2, 7, 16, 18, 20, 21 and 26; Figs 1a,b & 2d,f,h,j,k,p).

Additionally, the montane species Handleyomys intectus supports one 2.0° consensus area (area 1; Fig. 1a), and Nephelomys nimbosus supports three consensus areas in the 2.0° and 4.0° grid sizes (areas 2, 20 and 26; Figs 1b & 3j,p). Handleyomys fuscatus supports one 3.0° consensus area (area 7; Fig. 2d), and Microryzomys altissimus, Nephelomys albigularis, N. auriventer and N. meridensis support certain consensus areas in the 3.0° and 4.0° analyses (areas 4, 5, 6, 7, 14, 17, 18, 19, 20, 21 and 22; Figs 2a–d & 3d,g–l). Finally, Nephelomys devius, N. keaysi and N. levipes support certain 4.0° consensus areas (areas 14, 25 and 30; Fig. 3d,o,t).

The cis-Andean lowland forest species Neacomys musseri, N. minutus, N. spinosus, Oecomys superans and O. trinitatis support certain 3.0° and 4.0° consensus areas (areas 6, 8, 14, 20, 22 and 23; Figs 2c,e & 3d,j,l,m). The lowland forest species Scolomys ucayalensis and Nectomys apicalis also support additional 3.0° and 4.0° consensus areas (areas 6, 8, 17, 19, 20, 22 and 23; Figs 2c,e & 3d,g,i,j,l,m), and the presence of cis-Andean Euryoryzomys nitidus and trans-Andean species Melanomys caliginosus, Sigmodontomys alfari, Tanyuromys aphrastus and Transandinomys bolivaris define certain 4.0° consensus areas (areas 11, 12, 15, 16, 25 and 30; Fig. 3a,b,e,f, o,t).

The areas with the greatest endemicity values were located mainly in central-north Andes and were found in the 4.0° grid size (Table 1, area 20, score = 4.15385; area 23, score = 4.57500; area 26, score = 4.75962); additional details

Table 1 Summary of information on the consensus areas of the tribe Oryzomyini in South America, with information on the species composition with their respective score, number of cells for each area, the maximum scores and the grid sizes of each consensus areas. All consensus areas include only one area of endemism, except those with * which contain two areas. The ** observed in the column number of cells, indicates areas in which the cell of such consensus areas are disjunct.

Consensus areas	Endemic species (score)	Number of cells	Maximum score	Grid size
1	Handleyomys intectus (0.667); Nephelomys childi (0.764); Nephelomys pectoralis (1.000); Zygodontomys brunneus (1.000)	6	3.68056	2
2	Nephelomys nimbosus (0.700); Oreoryzomys balneator (0.700); Scolomys melanops (0.762)	5	2.38846	2
3	Aegialomys galapagoensis (1.000); Nesoryzomys indefessus (1.000); Nesoryzomys swarthi (1.000)	2	3.25000	2
4	Nephelomys albigularis (0.677); Oreoryzomys balneator (0.800); Scolomys melanops (0.677)	5	2.40385	3
5	Microryzomys altissimus (0.616); Nephelomys albigularis (0.900); Oreoryzomys balneator (0.800)	5	2.56579	3
6*	Microryzomys altissimus (0.545); Neacomys spinosus (0.511); Nectomys apicalis (0.591); Nephelomys albigularis (0.625); Nephelomys auriventer (0.625); Nephelomys albigularis (0.625); Scolomys ucayalensis (0.511)	9**	3.65909	3
7	Handleyomys fuscatus (0.750); Nephelomys childi (0.750); Nephelomys meridensis (0.643); Nephelomys pectoralis (0.750); Zygodontomys brunneus (0.750)	4	3.89286	3
8	Neacomys minutus (0.643); Neacomys musseri (0.643); Scolomys ucayalensis (0.750); Oecomys trinitatis (0.750); Oecomys superans (0.750)	4	3.78571	3
9	Cerradomys vivoi (0.800); Hylaeamys seuanezi (0.800); Oligoryzomys stramineus (0.650)	10	2.50000	3
10	Neacomys paracou (0.768); Oecomys rutilus (0.773); Oecomys auyantepui (0.808)	11**	2.59848	3
11	Tanyuromys aphrastus (0.688); Sigmodontomys alfari (0.813); Melanomys caliginosus (0.400); Transandinomys bolivaris (0.750)	8	2.90000	4
12	Sigmodontomys alfari (0.750); Melanomys caliginosus (0.475); Transandinomys bolivaris (0.900)	10	2.37500	4
13	Cerradomys subflavus (0.636); Drymoreomys albimaculatus (0.667); Oecomys catherinae (0.611)	9	2.41414	4
14	Neacomys musseri (0.578); Nephelomys auriventer (0.667); Nephelomys keaysi (0.500); Nephelomys levipes (0.550)	6	2.54444	4
15	Tanyuromys aphrastus (0.650); Melanomys caliginosus (0.818); Transandinomys bolivaris (0.695)	10	2.41364	4
16	Tanyuromys aphrastus (0.625); Nephelomys pectoralis (0.875); Nephelomys childi (0.729); Zygodontomys brunneus (0.875)	4	3.35417	4
17	Aegialomys xanthaeolus (0.673); Microryzomys altissimus (0.769); Nectomys apicalis (0.769)	13	2.46154	4
18*	Nephelomys childi (0.716–0.740); Nephelomys meridensis (0.614–0.635); Nephelomys pectoralis (0.875); Zygodontomys brunneus (0.875)	5	3.32955	4
19	Aegialomys xanthaeolus (0.707); Microryzomys altissimus (0.632); Nectomys apicalis (0.632); Nephelomys albigularis (0.727); Nephelomys auriventer (0.591)	11	3.53926	4
20	Microryzomys altissimus (0.337); Neacomys spinosus (0.606); Nephelomys albigularis (0.404); Nephelomys nimbosus (0.750); Oreoryzomys balneator (0.875); Scolomys melanops (0.875); Scolomys ucayalensis (0.635)	4	4.15385	4
21	Nephelomys meridensis (0.800); Nephelomys pectoralis (0.544); Oryzomys gorgasi (0.700); Zygodontomys brunneus (0.544)	5	3.83889	4
22	Aegialomys xanthaeolus (0.449); Microryzomys altissimus (0.705); Neacomys spinosus (0.462); Nectomys apicalis (0.705); Nephelomys albigularis (0.778); Nephelomys auriventer (0.611)	9	3.95940	4
23	Neacomys minutus (0.650); Neacomys musseri (0.650); Neacomys spinosus (0.867); Scolomys ucayalensis (0.650); Oecomys trinitatis (0.758); Oecomys superans (0.750)	4	4.57500	4
24	Neacomys paracou (0.672); Oecomys rutilus (0.917); Oecomys auyantepui (1.000)	6**	2.83889	4
25	Tanyuromys aphrastus (0.525); Sigmodontomys alfari (1.000); Nephelomys devius (0.700)	5	2.47500	4
26	Nephelomys childi (0.740); Nephelomys nimbosus (0.750); Nephelomys pectoralis (0.875); Oreoryzomys balneator (0.635); Scolomys melanops (0.635); Zygodontomys brunneus (0.875)	4	4.75962	4
27	Cerradomys vivoi (0.408); Oligoryzomys moojeni (0.750); Oligoryzomys rupestris (0.750); Oligoryzomys stramineus (0.650)	4	2.80833	4
28	Aegialomys galapagoensis (1.000); Nesoryzomys indefessus (1.000); Nesoryzomys swarthi (1.000)	2	3.25000	4
29	Sooretamys angouya (0.912); Euryoryzomys russatus (0.853); Oligoryzomys nigripes (0.912)	17	2.92647	4
30	Nephelomys keaysi (0.818); Nephelomys levipes (0.727); Euryoryzomys nitidus (0.875)	11	2.67045	4
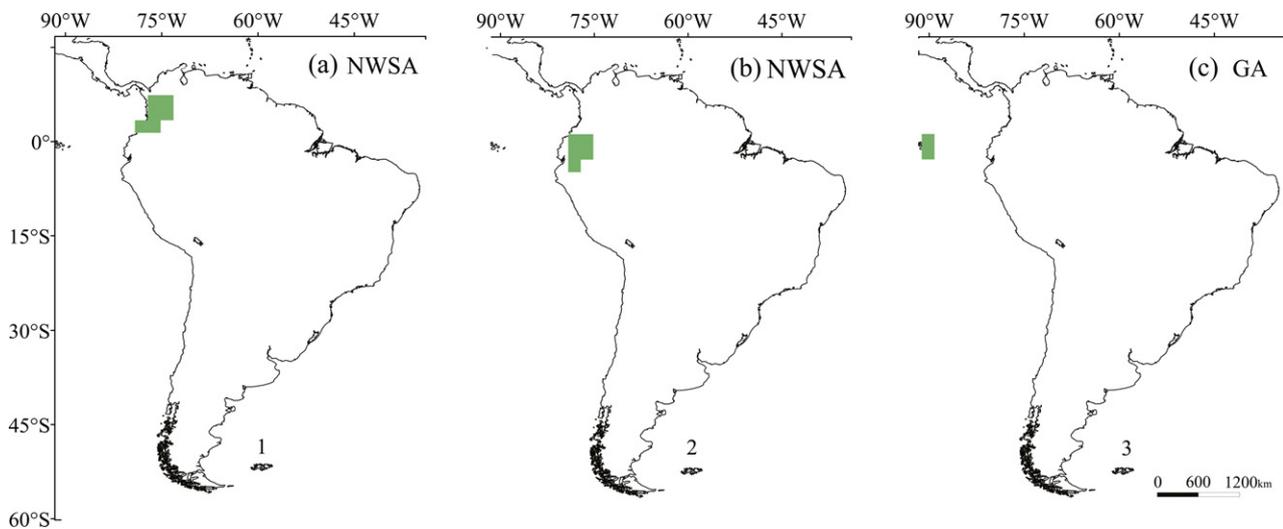
Figure 1 Consensus areas of endemism detected for oryzomyine rodents by NDM/VNDM using 2.0° grid size in South America. Areas of endemism: north-western South America, NWSA; Galápagos archipelago, GA.
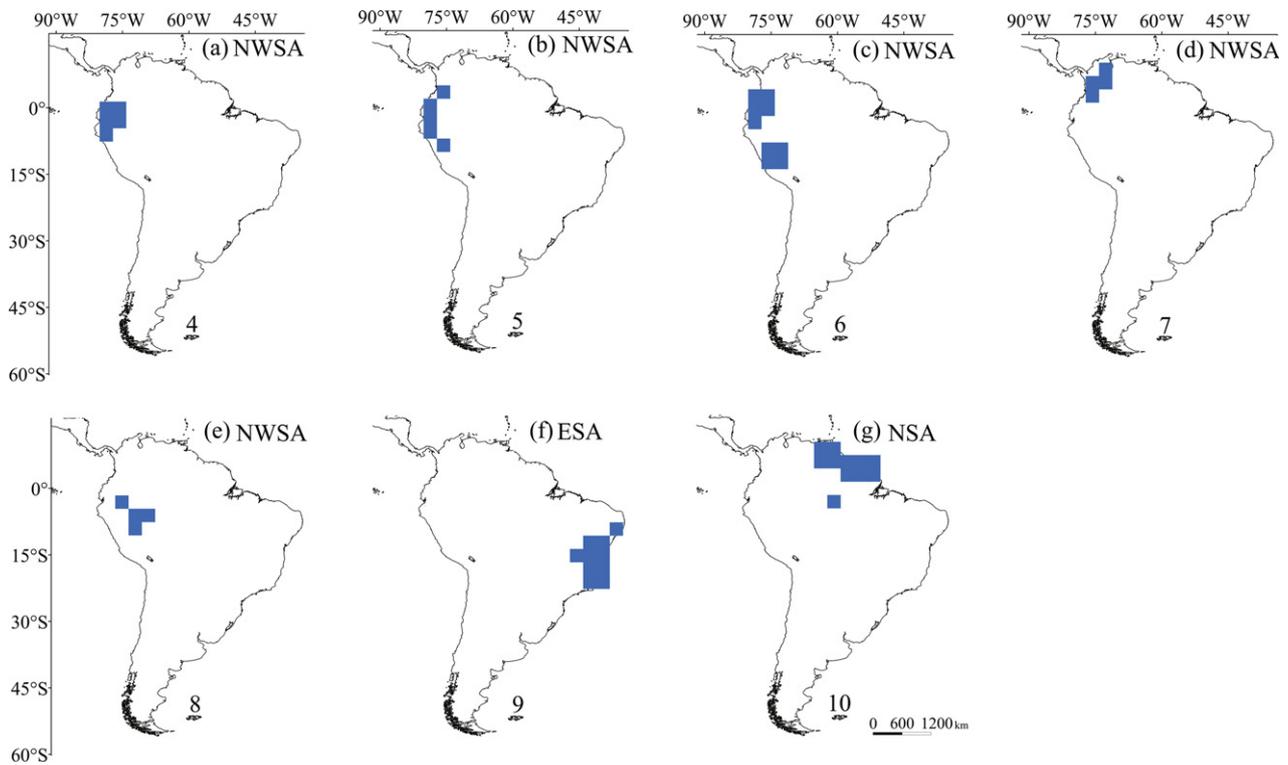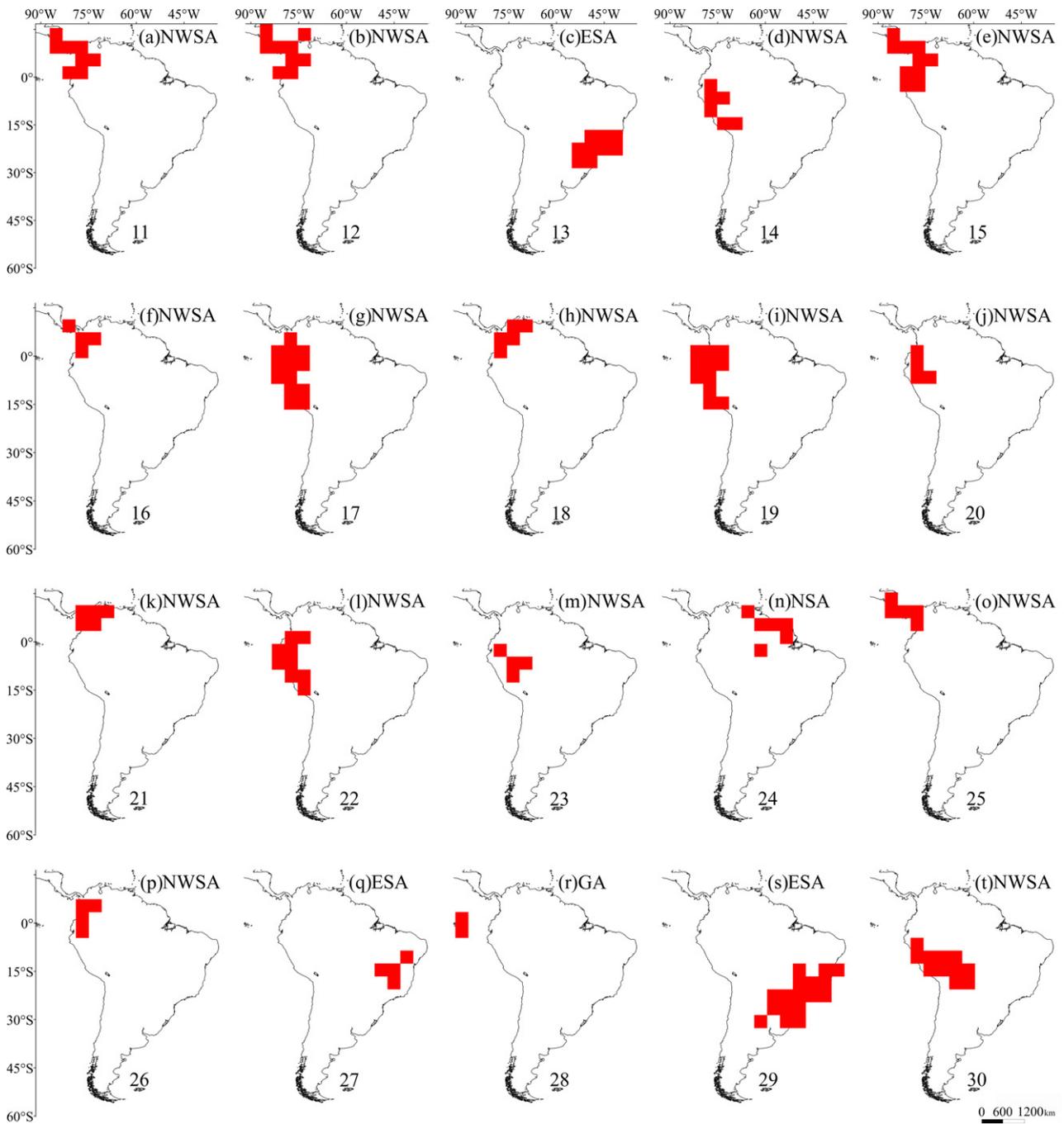

Figure 2 Consensus areas of endemism detected for oryzomyine rodents by NDM/VNDM using 3.0° grid size in South America. Areas of endemism: north-western South America, NWSA; eastern South America, ESA; northern South America, NSA.

regarding the supporting species of these areas are provided in Table 1.

Eastern South America (ESA)

ESA included consensus areas that were detected by two grid sizes (3.0° and 4.0°; Figs 2 & 3). One consensus area was identified by NDM/VNDM in 3.0° (area 9; Fig. 2f), and three consensus areas were identified in the 4.0° grid size (areas 13, 27 and 29; Fig. 3c,q,s). The areas of each grid are partly overlapped (Figs 2 & 3), although the supporting species detected for each grid size were different. *Hylaeamys seuanezi* supports one 3.0° consensus area (area 9; Fig. 2f), whereas *Cerradomys vivoi* and *Oligoryzomys stramineus* support one

Figure 3 Consensus areas of endemism detected for oryzomyine rodents by NDM/VNDM using 4.0° grid size in South America. Areas of endemism: north-western South America, NWSA; eastern South America, ESA; northern South America, NSA; Galápagos archipelago, GA.

consensus area in the 3.0° grid size and one consensus area in the 4.0° grid (areas 9 and 27; Figs 2f & 3q). In the 4.0° grid size, *Cerradomys subflavus, Drymoreomys albimaculatus* and *Oecomys catherinae* support one consensus area (area 13; Fig. 3c), while *Oligoryzomys moojeni* and *O. rupestris* provide support for one consensus area (area 27; Fig. 3q). *Euryoryzomys russatus, Oligoryzomys nigripes* and *Sooretamys angouya* support only area 29, in the 4.0° grid size.

The areas with the greatest endemicity values were located in south-eastern Brazil, Paraguay, and the northern portions of Uruguay and Argentina and were found in the 4.0° grid size (Table 1, area 29, score = 2.92647); additional details regarding the supporting species of these areas are listed in Table 1.

Northern South America (NSA)

Searches conducted in NDM/VNDM found only one consensus area for each 3.0° and 4.0° grid (area 10, score = 2.59848; area 24, score = 2.83889), and these areas overlap almost entirely (Figs 2g & 3n). The species that support these two
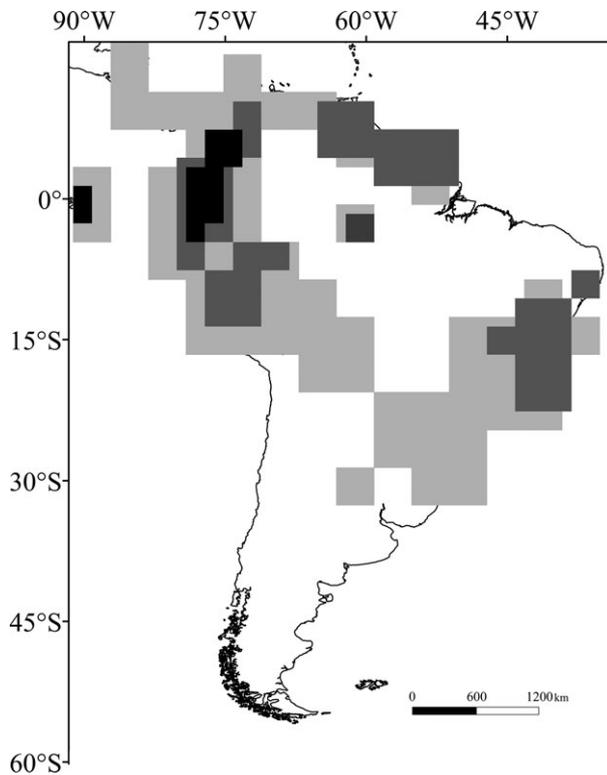
Figure 4 Overlap of the consensus areas of endemism detected for oryzomyine rodents by NDM/VNDM using 2.0° (black squares), 3.0° (dark grey) and 4.0° (light grey) grid sizes in South America.

consensus areas were the same for both grids sizes: *Neacomys paracou*, *Oecomys rutilus* and *O. auyantepui* (Table 1).

Galápagos archipelago (GA)

Areas of endemism were identified in the GA in grid sizes of 2.0° (area 3, score = 3.25) and 4.0° (area 28, score = 3.25) (Figs 1c & 3r). The species *Aegialomys galapagoensis*, *Nesoryzomys indefessus* and *N. swarthi* support this result in both grid sizes.

DISCUSSION

Species richness and the areas of endemism of oryzomyine rodents

Our database recovered four generalized areas of endemism for the tribe Oryzomyini in South America. Three of these are extensive and continental: north-western South America (NWSA), eastern South America (ESA), and northern South America (NSA). The fourth area, the Galápagos archipelago (GA), is an oceanic insular region. Each of the three continental regions encompasses part of one of the important mountain chains in South America: the Andean Cordilleras, the Oriental portion of the Brazilian Shield (Serra do Mar), and the Guyanan Shield, respectively.

Areas of endemism that obtained the highest endemicity scores included species from different habitat types. The NWSA comprises several vegetation types: the Lomas, the more open and drier vegetation that occurs in the western cordilleras in Peru and Ecuador; the Dry Forests, covering south-western Ecuador, the Huancabamba depression, and certain interior valleys in Peru and Bolivia; the Páramo vegetation, in northern Ecuador, Colombia and Venezuela between 2600 and 3800 m, above the tree line; the Sub-Páramo, which occurs sporadically from Colombia to Bolivia at elevations between 2700 to 3500 m; the Puna, from southern Ecuador to northern Argentina; the Cloud Forest, present on the oriental and some occidental Andean slopes from Venezuela to Bolivia between 1000 to 3800 m elevation; the Lowland Rain Forest, present up to 1000 m elevation from Central America to Peru; and finally, the deep valley vegetation, which covers the high inter-Andean valleys that are predominantly covered by grasses and crops (Hueck, 1972; Duellman, 1979). However, within NWSA, the area with highest endemism score in the three grid sizes mainly consisted of species from similar habitats (montane Andean Forests), but from distinct Andean slopes or sections, that are isolated by deep unforested valleys and open Páramo vegetation: *Nephelomys childi* and *N. pectoralis* occur in forested areas above 1100 m in Central, Oriental and Occidental cordilleras; *N. meridensis*, which is endemic to the northeastern Cordillera Oriental from 1100 to 4000 m elevation (Prado & Percequillo, 2013); and *Handleyomys fuscatus*, which is endemic to the north Andean region and inhabits the montane forest of the Andes from 1700 to 2700 m elevation (Prado & Percequillo, 2013). *Zygodontomys brunneus* is distributed through Andean, cis- and trans-Andean regions, in the open landscapes of the intermontane valleys of the northern Andes, which present elevational ranges from 350 to 1300 m (Prado & Percequillo, 2013).

ESA comprises the Atlantic Forest biome in eastern Brazil and Paraguay and the Misiones Province, Argentina; the southernmost portion of the Cerrado biome in central Brazil; the easternmost portion of Caatinga, in transition areas with Atlantic Forest; a small portion of the Pampas biome in southern Brazil and Uruguay; and parts of the Espinal and Chaco biomes on north-eastern Argentina (Hueck, 1972). Nevertheless, ESA includes species that are mainly distributed in the Atlantic Forest (*Hylaemys seuanezi*, *Drymoreomys albimaculatus*, *Oecomys catherinae*, *Euryoryzomys russatus* and *Sooretamys angouya*) and some that are found in the transitional vegetation between Atlantic Forest, Cerrado and Caatinga biomes (*Cerradomys vivoi*, *C. subflavus*, *Oligoryzomys stramineus*, *O. moojeni*, *O. rupestris* and *O. nigripes*) (Prado & Percequillo, 2013).

NSA encompasses the geological Guyanan Shield, extending southwards into Brazil east of Rio Negro and north of the Amazon River and further west into Colombia to Serranía Chiribiquete (Lim, 2012). Although lowland rain forest (with or without seasonal flooding) is predominant here, the area also includes extensive grasslands: the llanos of

Venezuela, the continuous area formed by the Rupununi, Rio Branco, and Gran Sabana of Guyana, Brazil and Venezuela, as well as a patch from the Sipaliwini and Brazilian border (Lim, 2012). In NSA, the species responsible for supporting this area of endemism for the tribe Oryzomyini are widely distributed in the forested areas: *Neacomys paracou*, *Oecomys auyantepui* and *O. rutilus* present similar distributions, with collection localities extending from the Atlantic Ocean westwards to the left bank of Rio Negro and southwards to the Amazon River (Prado & Percequillo, 2013). These species are considered endemic to the Guyanan Shield (Lim, 2012) and occur mainly in well-drained and swampy primary forest (Voss *et al.*, 2001).

The islands of the Galápagos archipelago with higher elevations have forested, humid areas associated with orographic moisture, and the extensive dry lowlands exhibit a landscape with sparse grassland (Trueman *et al.*, 2013). The GA area of endemism is supported by two species that occur on different islands: *Aegialomys galapagoensis* on Isla Santa Fé, Isla San Cristóbal and Isla Santiago; *Nesoryzomys swarthi* on Isla Santa Fé and Isla Santiago. We cautiously consider *N. indefessus* as a supporting species, as it is isolated on Isla Baltra and Isla Santa Cruz, not overlapping its distributional range with the other two species. We did not discard this as a supporting species since the area unit of the algorithm are defined by cells, that, albeit smaller, cluster different islands as a continuous area and as the Galápagos archipelago does not share any species of oryzomyine with the continent, the area and the supporting species represent a well-established area of endemism, under the criteria employed here. These species are always associated with xeric scrub (Prado & Percequillo, 2013).

The effects of grid sizes in the NDM/VNDM analyses

It is well known that grid size directly affects the results of NDM/VNDM analyses, as different sizes of cells can generate distinct hypotheses for areas of endemism, both in composition and coverage (Szumik *et al.*, 2002, 2012; Aagesen *et al.*, 2009). According to Szumik *et al.* (2002), very small grid cells will make all distributions entirely discontinuous, and then only very small areas of endemism or none at all will be recognized. In contrast, very large grid cells are likely to recognize very large areas of endemism, with many species appearing as endemic in each area. Moreover, the effect of grid size is directly correlated with the number and dispersion of the localities (see Szumik *et al.*, 2012).

Our results, employing a less diverse database over a continental area, are in concordance with the above expectations. NWSA was only the area of endemism recovered in the continental South America employing the 2.0° grid in the NDM searches, with few species supporting the obtained areas. By increasing the size of the cells, the number of areas of endemism also increased, with the 4.0° grid resulting in the hypothesis of a high number of areas of endemism that overlapped over almost the entire South American continent

(Fig. 3). The exceptions are the areas on the northern and southern banks of the Amazon River, extensive portions of the continent where sampling is still inadequate (see Prado & Percequillo, 2013; Fig. 3). Probably because we employed a less diverse database with few cases of sympatry at the species level, the method failed to recover additional areas with the smaller cell grid size and exaggerated the recognition of an elevated number of areas with the larger cells.

The smallest cell size employed identified Andean areas of endemism, although with limited sympatry. This result was obtained because these areas exhibit a higher number of more exclusive species for oryzomyine rodents in a small area, mainly due the elevational gradient (see Ferro, 2013) and high diversity of habitats in small patches (Patterson *et al.*, 2012). In contrast, the detection of areas of endemism through an environmental gradient that varies along the latitude or longitude (instead of elevation), as occurs in the NSA and ESA, demands larger grid sizes.

Had we chosen only one grid size to search for areas of endemism, we would not have been able to evaluate and discuss the patterns of endemism throughout the continent, because different grid sizes recovered distinct (although sometimes overlapping) areas of endemism in South America. Considering our results, the use of smaller grid cells appears to be more restrictive and rigorous, generating only three areas of endemism, each of which exhibits unique and diversified faunas (see Prado & Percequillo, 2013). However, important areas in eastern South America were not recovered as endemic with smaller grids, although they exhibited endemic oryzomyine fauna in a traditional biogeographical approach (see Weksler, 2006; Prado & Percequillo, 2013). One possible explanation of these results is that with less diverse datasets on a continental scale the NDM algorithm, using small grids, experiences some difficulty in the recognition of areas of endemism; future approaches, employing other tribes of Sigmodontinae would allow this hypothesis to be tested. On the other hand, the use of larger grid cells recovered vast areas of endemism: our hypothesised areas of endemism comprise elements from different habitats (even on smaller grid sizes), including species from transitional areas between forest and open habitats, i.e. our areas transcend the limits of the biomes that are currently recognized (e.g. ESA, that exhibit Atlantic Forest and Cerrado forms as supporting species). This is probably a consequence of the past common history among taxa that currently inhabit these biomes (such as species of the genus *Oligoryzomys*, as well as the genera *Cerradomys* and *Sooretamys*; see Parada *et al.*, 2013), but whose ancestors lived in transitional, less clearly identifiable, areas as a consequence of climatic and vegetation changes in South America, as modelled by Vivo & Carmignotto (2004).

Areas of endemism and species richness in South America

NWSA exhibits the greatest number of consensus areas of the three grid sizes overlapped, and it covers the southern

region of Central America, Ecuador, south-central to northern Peru, and part of western Amazonia. This region is considered biogeographically important by other authors such as Cracraft (1985) and Morrone (2001, 2014), who reported various areas of endemism for birds and several other organisms, respectively, in the same region, i.e. the Tumbesian Centre, equivalent to part of Tumbes-Piura Province; North Andean Centre, equivalent to the Occidente de Ecuador and Cauca Provinces of Caribbean subregion and Páramo Norandino Province of Andean Subregion; Peruvian Andes Centre, similar to Yungas and partially to Ucayali Provinces of Amazonian subregion; Peruvian Arid Coastal Centre, partly similar to a portion of Tumbes-Piura Province and also to Desierto Peruano Costeiro Province of Andean Subregion; Marañón Centre, partly similar to Ucayali Province; and Chocó and Magdalena Centre, both identically named by Morrone (2001, 2014). Reig (1986) and Nores (2004) also found a high rodent and avian diversity, respectively, in the northern Andean region, recognizing areas of endemism in this region; Reig (1986) even recognized the northern portion of the Andes as the 'area of original differentiation' (AOD) for the tribe Oryzomyini. Additionally, Amori *et al.* (2013) reported that the western margins of the Amazon Basin include one of the three most important areas of rodent richness in South America, a pattern also observed by Prado & Percequillo (2013) for oryzomyine rodents.

The existence of the ESA area of endemism is in accordance with the biodiversity patterns reported for the region. The ESA is represented predominantly by the Atlantic Forest, which has long been claimed to be a region of endemism for many plants, invertebrate and vertebrate groups and is considered one of the most important forests worldwide for conservation priorities, being a biodiversity hotspot (Costa *et al.*, 2000; Myers *et al.*, 2000; Mittermeier *et al.*, 2005). This area also includes a part of the region cited in Amori *et al.* (2013) and Prado & Percequillo (2013), which is one of the three major regions for rodent richness in South America. Four of the areas of endemism proposed by Cracraft (1985) and Morrone (2001, 2014) are congruent with the ESA: Serra do Mar Centre and Bosque Atlántico Brasileño Province; Paraná Centre and Bosque Paranaense Province; Campo Cerrado Centre and Cerrado Province; and Caatinga Centre and Province.

Since the pioneering study of Wallace (1852), NSA has been considered a distinct biogeographical area in South America (Haffer & Prance, 2001). A recent summary of the biogeography of mammals from Guianas suggested that the ancient Guyanan Shield craton plays a potential role as a stable core area for biotic diversification (Fouquet *et al.*, 2012; Lim, 2012). The area of endemism identified for birds (Cracraft, 1985) is the Guyanan Centre that is equivalent to the Guyana Húmeda Province and partially similar to the Amapá and Roraima Provinces. According to Amori *et al.* (2013) and Prado & Percequillo (2013) the Guyanan Shield craton is one of the three most important areas for rodent richness.

Endemism, and the tempo and mode of evolution of oryzomyine rodents

Some definitions of endemism involve the recognition of monophyletic lineages occupying exclusive areas (see Parenti & Ebach, 2009), but such approach is not available for most taxa of tribe Oryzomyini, although some comments can be addressed based on recent phylogenetic contributions (Machado *et al.*, 2013; Parada *et al.*, 2013). The taxa of the GA area, *Aegialomys* and *Nesoryzomys*, sister taxa according to Parada *et al.* (2013), probably share a common history after the origin of the archipelago about 4 Ma (Grehan, 2001). Given that *Aegialomys* presents species on both the continent and on the islands, and has an ambiguous ancestral area of distribution, two alternative explanations can be proposed: both genera originated on the continent and colonized the islands through waif dispersal around 2.5 Ma (Parada *et al.*, 2013), and the genus *Nesoryzomys* subsequently became extinct on the continent; or the ancestor split into subordinate taxa on the Galápagos archipelago about 2.5 Ma, with the dispersion of *Aegialomys* to the continent afterwards. As oceanic currents move northwards from Peru (area of distribution of *Aegialoms xanthaeolus*, *A. baroni* and *A. ica*) to the Galápagos (Le Roux, 2012), the first proposal seems more likely.

The NWSA area exhibits several species of the genus *Nephelomys* and one species of the genus *Handleyomys*, montane forest genera from Andean region that are each other's closest relatives; these two genera are sister to a lowland clade formed by *Hylaeamys* and *Oecomys* (Parada *et al.*, 2013) and the divergence between montane and lowland forms occurred around the early Pliocene, *c.* 5 Ma. This period is coincident with the major tectonic activity of Andean orogenesis on northern Andes, which occurred from 7 to 2.5 Ma (Hoorn *et al.*, 2010); afterwards, the montane lineages diverged at least 4.5 Ma, latitudinally and probably elevationally along the Andean Cordillera.

The endemic lineages of ESA and NSA do not share a common evolutionary and biogeographical history because they are dispersed in several clades of the tribe: *Cerradomys*, *Euryoryzomys*, *Neacomys*, *Oecomys* and *Oligoryzomys* belonging to three distinct clades; *Drymoreomys*, an Atlantic Forest genus, is the sister taxa of *Eremoryzomys*, a taxon inhabiting the dry areas of the upper Marañon River, with a possible cladogenesis event about 4 Ma. Nevertheless, although these lineages belong to distinct phylogroups, their origin is contemporary: the ancestral nodes for *Euryoryzomys*, *Hylaeamys* and *Oecomys* were hypothesized for 4.2 Ma, with a confidence interval from 3 to 5 Ma. A possible exception involves *Sooretamys* and *Cerradomys*, the only lineages that exhibit a sister-taxa relationship: the split between the Atlantic Forest and the Cerrado genera, respectively, probably occurred around 4.5 Ma (between 3 and 6 Ma; Parada *et al.*, 2013).

Although important areas of South America remain inadequately sampled, available data in museums worldwide

allowed us, after a careful species identification effort and search for adequate geographical information, to elaborate a substantial database on oryzomyine species richness and geographical distribution. Through this database, regardless of the grid size employed with NDM/VNDM, we established the first hypotheses regarding the presence of areas of endemism of the Oryzomyini tribe in South America. These areas are similar to those that were recovered using other, more taxonomically diverse, datasets (Müller, 1973; Cracraft, 1985; Morrone, 2001, 2014), and are more complete and adequate than those previously defined (Reig, 1986; Valencia-Pacheco *et al.*, 2011). Given that some areas of endemism are sustained by presumably monophyletic lineages (as *Aegialomys* and *Nesoryzomys* in GA, and *Nephelomys* and *Handleyomys* in NWSA; Parada *et al.*, 2013), we could hypothesize that the origin of these areas and their component taxa are resultant of the same events in time and space. This expectation should be more exhaustively tested in the future, with new distributional data and more comprehensive studies on the genealogical relationships of the species inhabiting these areas (Santos & Amorin, 2007). Therefore, for now, we have provided an important and fundamental step for the identification of areas of endemism, contributing to a better knowledge of the biogeography of the tribe Oryzomyini in South America.

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BIOSKETCH

The studies conducted at the Laboratório de Mamíferos at the Escola Superior de Agricultura 'Luiz de Queiroz', Universidade de São Paulo, coordinated by **Alexandre R. Percequillo,** are focused mainly on the systematics and biogeography of the subfamily Sigmodontinae, as well as mammalian inventories, and studies on the ecology and natural history of rodents.

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