

Small mammal distributional patterns in Northwestern Argentina

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ABSTRACT. Quantitative evaluations of species distributional congruence allow evaluating previously proposed biogeographic regionalization and even identify undetected areas of endemism. The geographic scenery of Northwestern Argentina offers ideal conditions for the study of distributional patterns of species since the boundaries of a diverse group of biomes converge in a relatively small region, which also includes a diverse fauna of mammals. In this paper we applied a grid-based explicit method in order to recognize Patterns of Distributional Congruence (PDCs) and Areas of Endemism (AEs), and the species (native but non-endemic and endemic, respectively) that determine them. Also, we relate these distributional patterns to traditional biogeographic divisions of the study region and with a very recent phytogeographic study and we reconsider what previously rejected as 'spurious' areas. Finally, we assessed the generality of the patterns found. The analysis resulted in 165 consensus areas, characterized by seven species of marsupials, 28 species of bats, and 63 species of rodents, which represents a large percentage of the total species (10, 41, and 73, respectively). Twenty-five percent of the species that characterize consensus areas are endemic to the study region and define six AEs in strict sense while 12 PDCs are mainly defined by widely distributed species. While detailed quantitative analyses of plant species distribution data made by other authors does not result in units that correspond to Cabrera's phytogeographic divisions at this spatial scale, analyses of animal species distribution data does. We were able to identify previously unknown meaningful faunal patterns and more accurately define those already identified. We identify PDCs and AEs that conform Eastern Andean Slopes Patterns, Western High Andes Patterns, and Merged Eastern and Western Andean Slopes Patterns, some of which are re-interpreted at the light of known patterns of the endemic vascular flora. Endemism do not declines towards the south, but do declines towards the west of the study region. Peaks of endemism are found in the eastern Andean slopes in Jujuy and Tucumán/Catamarca, and in the western Andean biomes in Tucumán/Catamarca. The principal habitat types for endemic small mammal species are the eastern humid Andean slopes. Notwithstanding, arid/semi-arid biomes and humid landscapes are represented by the same number of AEs. Rodent species define 15 of the 18 General Patterns, and only in one they have no participation at all. Clearly, at this spatial scale, non-flying mammals, particularly rodents, are biogeographically more valuable species than flying mammals (bat species).

KEYWORDS. Chiroptera, Didelphimorphia, distributional congruence, geographical patterns, Rodentia.

RESUMEN. Patrones de endemismo de pequeños mamíferos en el Noroeste de Argentina. Las evaluaciones cuantitativas de congruencia distribucional de las especies permiten comparar regionalizaciones biogeográficas propuestas previamente e incluso identificar áreas de endemismo que no han sido detectadas. El escenario geográfico del Noroeste Argentino ofrece condiciones ideales para el estudio de patrones de distribución de especies. En este artículo aplicamos un método explícito basado en cuadrículas con el objetivo de reconocer Patrones de Congruencia Distribucional (PDCs) y Áreas de Endemismo (AEs), así como las especies (nativas pero no endémicas y endémicas, respectivamente) que las determinan, para examinar las relaciones de las especies de micromamíferos con las principales unidades ambientales. Adicionalmente, relacionamos estos patrones distribucionales con las divisiones biogeográficas tradicionales de la región estudiada y con un estudio fitogeográfico muy reciente y reconsideramos lo que previamente rechazamos como 'áreas espurias'. Finalmente, evaluamos la generalidad de los patrones encontrados. El análisis resultó en 165 áreas consenso, caracterizadas por siete especies de marsupiales, 28 especies de murciélagos y 63 especies de roedores, lo que representa un gran porcentaje del total de especies (10, 41 y 73, respectivamente). Veinticinco por ciento de las especies que caracterizan las áreas consenso son endémicas a la región estudiada y definen seis AEs en sentido estricto, mientras que 12 PDCs están principalmente definidos por especies ampliamente distribuidas. Mientras que los análisis cuantitativos de la distribución de especies de plantas no resultan en unidades que coincidan con las divisiones fitogeográficas de Cabrera a esta escala espacial, los análisis de la distribución de especies animales muestran patrones que sí se corresponden con tales divisiones. Identificamos patrones de distribución de la fauna significativos y definimos más adecuadamente aquellos ya identificados. Identificamos PDCs y AEs que conforman los Patrones de las Pendientes Andinas del Este, los Patrones Andinos Altos del Oeste y los Patrones de las Pendientes Andinas Este y Oeste Fusionados, algunos de los cuales son re-interpretados a la luz de patrones conocidos de la flora vascular endémica. El endemismo no declina hacia el sur, pero sí hacia el oeste de la región estudiada. Los picos de endemismo se encuentran en las pendientes del este de los Andes en Jujuy y Tucumán/Catamarca, y en los biomas andinos del oeste en Tucumán/Catamarca. El tipo de hábitat principal para las especies endémicas de mamíferos pequeños está en las pendientes húmedas del este de los Andes. A pesar de esto, los biomas áridos y semiáridos y los paisajes húmedos están representados por el mismo número de AEs. Las especies de Rodentia definen 15 de los 18 Patrones Generales (GPs), y sólo en uno de ellas no participaron. Claramente, a esta escala espacial, los mamíferos no voladores, particularmente los roedores, son biogeográficamente más valiosos que los mamíferos voladores.

PALABRAS CLAVE. Chiroptera, congruencia distribucional, Didelphimorphia, patrones geográficos, Rodentia.

An area of endemism (AE) is defined by the congruent geographical distribution of 2 or more species that are spatially restricted to this area (PLATNICK, 1991). This means that the non-random distributional congruence of two or more species results in an AE (CRISCI *et al.*, 2006). This definition implies sympatry, but not necessarily an

exact congruence of the distributions of the species involved (PLATNICK, 1991; MORRONE, 1994; MORRONE & CRISCI, 1995; see, for example, PERERA *et al.* (2011) for a qualitative biogeographical study of endemic fauna). Quantitative biogeographic methods to assess and characterize areas involve the processing of distributional data (locality

records) of the species (MURGUÍA & LLORENTE-BOUSQUETS, 2003). Several methods for identifying AEs proposed in recent years are based on PLATNICK (1991)'s definition. However, most methods traditionally applied to recognize AEs are non-spatially explicit. Conversely, SZUMIK *et al.* (2002) and SZUMIK & GOLOBOFF (2004) formalized a method that explicitly considers the spatial aspects of species distribution to identify AEs, evaluating the degree of overlap between the geographical distributions of species through the application of an optimality criterion (SZUMIK & ROIG-JUÑENT 2005).

Northern Argentina is a transition zone between the tropics and subtropics: the Tropic of Capricorn passes through Jujuy, Salta, and Formosa provinces in the north. Due to its tropical-subtropical location, Northwestern Argentina (NWA) provides a good opportunity to investigate some of the factors that can determine the distribution of species. The boundaries of a diverse group of biomes converge in a relatively small region, which also includes a diverse fauna of mammals. Moreover, NWA includes the largest portion of the southern central Andes, whose endemic vascular plant species distribution has been recently studied (AAGESEN *et al.*, 2012). In this sense, the geographic scenery of NWA offers ideal conditions for the study of distributional patterns of animal species and for comparisons between floral and faunal patterns. Also, specifically dealing with small mammals, the large phylogenetic divergence between the three orders that inhabit NWA allows testing the generality of the patterns found (in the present and in previous studies, particularly those of SANDOVAL *et al.*, 2010 and SANDOVAL & FERRO, 2014) and their transcendence to a small group of certain forms of life (i.e. a particular genus, family, order).

Although some studies have characterized the major South American and Argentinean biomes, including those represented in NWA, as distinctive biogeographic provinces (CABRERA & WILLINK, 1973; CABRERA, 1976; VERVOORST, 1979; among others), these characterizations were traditionally essentially qualitative, and most were based almost exclusively on its floristic components. For example, regarding the study of CABRERA (1976), which is almost invariably used by researchers working in Argentina when they need to assign the study area or flora to a phytogeographic unit, it proposes a hierarchical partition of the regions. However, the partition criteria Cabrera effectively applied is not explicit, and, although the author argues that he categorizes successive levels of the phytogeographic hierarchy by endemism and taxa predominance, in fact, the criteria are not exclusively taxonomic and are not always hierarchically applied (RIBICHICH, 2002). To characterize phytogeographical areas, the author refers to the extension of the types of vegetation, and to “what taxa of different ranks are alternately dominant, conspicuous, unique, important, frequent, endemic, dominant, abundant, distinctive, prominent, present, common, constant, typical, represented, accompanying, associated or co-dominant in the represented

area or ecological communities” (RIBICHICH, 2002), without presenting any formal definition of the meaning of such terms. In particular, Cabrera does not clarify what concept or what synonyms of endemic he used (RIBICHICH, 2002). For other than floristic taxa, with very few exceptions (e.g., DÍAZ GÓMEZ, 2007; LIZARRALDE & SZUMIK, 2007; AAGESEN *et al.*, 2009; NAVARRO *et al.*, 2009; SANDOVAL *et al.*, 2010; SZUMIK *et al.*, 2012; SANDOVAL & FERRO, 2014), these regions have been assumed as natural, and its congruence with the distribution of species was not tested. In fact, quantitative evaluations of species distributional congruence are very recent compared to narrative biogeographic regionalizations that have been made for decades by different naturalists. Quantitative approaches allow assessing previously proposed biogeographic regionalization and even identify previously undetected areas of endemism.

It has been previously assessed the classic phytogeographic regionalization of NWA by using small mammal distributional records (SANDOVAL *et al.*, 2010; SANDOVAL & FERRO, 2014) and the authors have been able to relate the obtained patterns to the traditional phytogeographic units within the region and to conclude that obtained distribution patterns in general concur with those units. However, in both cases they miss the opportunity of: (1) Analyzing the results obtained from mammal distributional data with those obtained by AAGESEN *et al.* (2012) in order to outline a more general biogeographical scheme for the region, i.e., an scheme that take into account both faunal and floristic elements. (2) To deeply discuss what previous works discarded as ‘spurious’ areas (i.e., patterns that merge highly divergent units, e.g., merging eastern and western Andean slopes, or humid and arid habitats; SANDOVAL & FERRO, 2014), considering that some of these ‘spurious’ areas may even include a higher portion of endemic species than the areas of endemism (AEs) that they did recognize (SANDOVAL & FERRO, 2014) and that some of these areas may also survive changes in grid size (one of the identified criterions for areas support; AAGESEN *et al.*, 2009; CASAGRANDA *et al.*, 2009; SZUMIK *et al.*, 2012; DASILVA *et al.*, 2015). Since AEs may or may not include a single biogeographic unit (e.g., the endemic flora of the region do not; AAGESEN *et al.*, 2012), we want to reassess the issue but seriously analyzing the AEs that were previously dismissed as spurious (SANDOVAL & FERRO, 2014). And (3) To address all small mammal distributional records in an integrated and comparative analysis to evaluate the distributional patterns of non-flying (i.e. marsupials and rodents) versus the patterns of flying small mammals (i.e. bats) (assessment outlined in SANDOVAL *et al.*, 2010). Bats and terrestrial small mammals (marsupials and rodents) exhibit disparate attributes, making them ideal for comparative purposes. Many bats have extensive ranges (LYONS & WILLIG, 1997). Actually, it has been mentioned that there is an apparently common pattern of low rates of endemism in several birds and bats that may be due to the high vagility of flying

versus non-flying vertebrates (MYERS & WETZEL, 1983). Contrary, most marsupials and rodents have relatively restricted ranges, probably due to their lack of vagility and poor dispersal abilities.

In this paper, we applied a grid-based explicit method to analyze distributional records of Northwestern Argentinean small mammal species in order to recognize patterns of species co-occurrence and the species that determine them. Also, we relate these distributional patterns to traditional biogeographic divisions of the study region and with a very recent phytogeographic study (AAGESEN *et al.*, 2012), and we reconsider what was previously rejected as 'spurious' areas (SANDOVAL & FERRO, 2014). Finally, we assessed the generality of the patterns found by evaluating the distributional patterns of non-flying versus the patterns of flying small mammals.

MATERIAL AND METHODS

Study region. The study region is located in the southern part of the central Andes. The tropical eastern slopes of the Andes are recurrently recognized as a continental and global hotspot of diversity and endemism for several taxa (e.g., RAHBK & GRAVES, 2001; BARTHOLOTT *et al.*, 2005; KIER *et al.*, 2005; ORME *et al.*, 2005; SKLENÁŘ *et al.*, 2011; PATTERSON *et al.*, 2012). The study region is located where the high diversity and endemism of the eastern Andes slopes gradually fade southward and comprises the northwestern portion of Argentina (NWA), including the political provinces of Jujuy, Salta, Tucumán, Catamarca, and Santiago del Estero (Fig. 1), between parallels $\sim 22^{\circ}\text{S}$ and $\sim 30^{\circ}\text{S}$, and meridians $\sim 62^{\circ}\text{W}$ and $\sim 69^{\circ}\text{W}$ (Fig. 1). The entire region comprises 470,184 km², which represents approximately 17% of the total Argentinean territory (2,791,810 km²).

Due its location between the tropical and subtropical latitudes and the complex relief, with the Andean orography on the western half of the region, which varies between 500 and 6000 m altitude, this region is characterized by

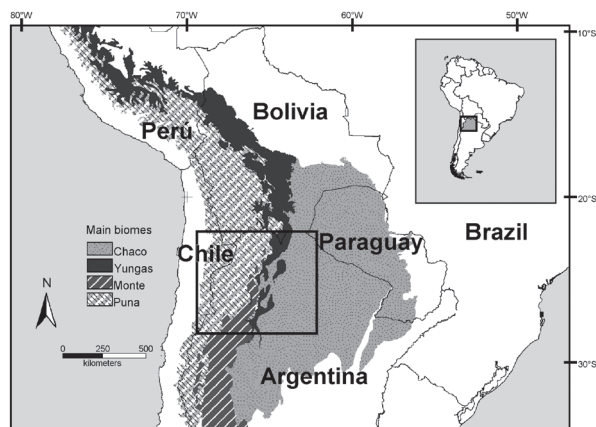


Fig. 1. Study region. The study region, Northwestern Argentina, is framed on a map that includes central and northern Argentina and Chile, southern Peru, Bolivia, Paraguay, and southern Brazil. In the upper right corner the map position in South America is indicated. The traditional major biogeographic divisions (Chaco, Yungas, Monte, and Puna) are included.

high environmental heterogeneity, great climatic contrasts and a mosaic of different biomes. All these biomes come together and some of them reach their limits of distribution in the region (CABRERA & WILLINK, 1973; CABRERA, 1976; BURKART *et al.*, 1999; MORRONE, 2001a).

The biogeographic description outlined below follows CABRERA (1976), BURKART *et al.* (1999) and MORRONE (2001a). The mountain ranges are located to the west and they are oriented north to south. The Sierras Subandinas, the Sierras Pampeanas, the Cordillera Oriental, and the Cordillera de los Andes are the substrate on which are developed the biomes of High Andes, Puna and Prepuna; while on its slopes and intermountain valleys are developed the xeric scrublands of the Monte, the montane rainforest of the Yungas, and the semiarid woodlands of the Chaco. The Sierras Subandinas and Pampeanas show an insular form and are surrounded by forests of Yungas and Chaco. The other mountain systems are relatively continuous, reach higher altitudes and separate the forest environments on the eastern slope of the open environments of Monte, Prepuna, Puna, and High Andes on the tops and the western slope. The eastern plains correspond to the Chaco biome.

Data set. The taxonomic treatment used herein basically follows that outlined in WILSON & REEDER (2005) and BARQUEZ *et al.* (2006). We used distributional information of 124 small mammal species (10 species of Didelphimorphia, 41 of Chiroptera, and 73 species of Rodentia), i.e., those species whose adults range in weight from four grams to two kilograms (WILSON *et al.* 1996) and inhabits North-western Argentina (Appendix and Supplementary Material).

The main source of data was the specimens reviewed in all the major systematic collections of Argentina (see Acknowledgements). We also completed the data including published localities of occurrence for small marsupials and bats, and for species of the rodent families Chinchillidae, Caviidae, Octodontidae, and Abrocomidae (DÍAZ & BARQUEZ, 2007; DÍAZ *et al.*, 2000; JAYAT *et al.*, 2009; JAYAT *et al.*, 2013; JAYAT & ORTIZ, 2010; MARES *et al.*, 1997), which have very few specimens based records and have no major problems with their alpha taxonomy. The complexity of the taxonomic history of most other species of Rodentia and the variety of approaches taken by different authors as to the limits of each taxa make very difficult to compare the entities mentioned in the literature with those considered in this paper.

Localities were taken from museum tags or from collector catalogues. All localities were checked and georeferenced using gazetteers, maps, or satellite images and field trips. We agree with TABENI *et al.* (2004) in the use of georeferenced records to optimize the quality of the analysis, contrary to the use of distributional maps for the species, which tend to overestimate species diversity in the regions under study (but see SOBERÓN *et al.*, 2000).

Finally, we divided the species into two classes according to its distributional range, restricted to the study region and widely distributed.

Distributional analyses. The method used to identify the AEs and Patterns of Distributional Congruence (PDCs) of small mammals in Northwestern Argentina was proposed by SZUMIK *et al.* (2002) and SZUMIK & GOLOBOFF (2004). This method implements an optimality criterion that explicitly considers the spatial location of the species in the study region. The study region is divided into cells, and the sets of cells (=candidate areas; AAGESEN *et al.*, 2013) are evaluated through an index of endemism. Individual values of endemism between 0 and 1 are calculated for each species depending on the fit of the species geographical distribution to the candidate area being evaluated. Individual values are combined for all the species that contribute to a set to obtain the value of endemism (score) of the area. The analysis results in a number of areas with maximum scores. This optimality criterion is implemented in the computer program NDM and its viewer VNDM (GOLOBOFF, 2005; available at <http://www.lillo.org.ar/phylogeny/>). As SANDOVAL & FERRO (2014), we will consider basically two areas categories: areas of endemism (AEs, defined only or mostly by sympatric endemic species) and local patterns of distributional congruence (PDCs, defined only or mostly by sympatric species not endemic to the study region). It should be noted that the optimality criterion that was used is based on the classic concept of areas of endemism. Therefore, ideally, the taxa to be used in such an analysis of endemism should be those that are maximally endemic, i.e., those whose geographic ranges are smaller than the study region. Even so, the method can be extended to be applied in the search for patterns of distributional congruence determined both by species of restricted ranges (i.e., AEs) as by widely distributed species whose ranges exceed the study region (AAGESEN *et al.*, 2009), which will constitute local patterns of distributional congruence (PDCs) but not AEs in strict sense. While AEs in strict sense provide strong basis for biogeographic regionalization, PDCs provide first-step testable hypotheses of AEs for future analyses of neighbouring regions or analyses at more inclusive scales (SZUMIK *et al.*, 2012). The distributional congruence of non-endemic species may be representing parts of larger AEs, local co-occurrence by particular combinations of ecological or climatic factors, or an artifact due to unevenness of sampling localities. It is beyond the purposes of this study to identify the causal factors of the distributional concordances identified. Whether the factors restricting the species ranges are a combination of present day ecological and physical phenomena or consequence of a history of vicariance and speciation, it is not a prerequisite for the detection of the pattern, which is, in turn, the first step in the elucidation of the process generating them (SANDOVAL & FERRO, 2014). As AAGESEN *et al.* (2009), we use the optimality criterion to analyze species distribution in a regional context while relaxing the criterion of endemism. Accordingly, we will treat the scoring species as characterizing and not always as endemic species: the scoring species may be involved in the characterization of an area being or not being endemic

or exclusive to that area.

We performed analyses with five different databases: first, one with a dataset that comprises all the small mammal species (SM database, 124 species); then, with a dataset that comprise terrestrial small mammals (orders Didelphimorphia and Rodentia; TSM, 83 species); and finally, three analyses, each comprising the species of Didelphimorphia, Chiroptera, and Rodentia separately (Di, 10 species, Ch, 41 species, and Ro, 73 species). Because there is no formal argument to use only one grid cell size (AAGESEN *et al.*, 2009; CASAGRANDA *et al.*, 2009), we analyzed the matrix of georeferenced data using grid cells of four different sizes (1, 0.75, 0.5, and 0.25° latitude-longitude). The use of several grid sizes increases the chance of finding different areas given the topographical complexity of the study region; moreover, using several grid sizes provides some kind of measure of support for a particular area of endemism: those areas which survive changes in grid size can be considered more strongly and clearly supported by the data (AAGESEN *et al.*, 2009; CASAGRANDA *et al.*, 2009; SZUMIK *et al.*, 2012; DASILVA *et al.*, 2015; although some very restricted areas can be strongly supported by the data, but would not be found by larger grids; Augusto Ferrari, com. pers.). Additionally, grid sizes used in this analysis were already used for the study region facilitating comparisons with previous studies (e.g., AAGESEN *et al.*, 2009; DÍAZ GÓMEZ, 2007; NAVARRO *et al.*, 2009; SANDOVAL *et al.*, 2010; SANDOVAL & FERRO, 2014; SZUMIK *et al.*, 2012). If the cells are too small the number of artificially empty cells increases and reduce the number of sympatric species, preventing correct detection of AEs. The practical problem with fine grids is that available data are usually incomplete including many gaps. To counteract this, we established filling values, which minimize the number of empty cells (ARIAS *et al.*, 2011; CASAGRANDA *et al.*, 2009; SZUMIK & GOLOBOFF, 2004). Therefore, we analyzed our matrix considering different filling values for assumed and inferred presences for smaller cells (square cells of 0.5° and 0.25° per side; Tab I). An assumed presence implies that, even if a species has not been recorded in a cell, its presence, although unconfirmed, is suspected or assumed by the user due to its proximity to records in neighbouring cells (SZUMIK & GOLOBOFF, 2004). An inferred presence is implemented by the method itself when a species is absent from a cell but present in surrounding cells (SZUMIK & GOLOBOFF, 2004). Therefore, as SZUMIK & GOLOBOFF (2004) highlighted, the assumed presences are given prior to the analysis, whereas the inferred presences are postulated as part of the analysis. Not setting filling values for the analysis of data when using grids with larger cell sizes is based on the fact that density of points of occurrence in relation to the proportion of the study region that is covered by a cell of large size makes it unnecessary. For a brief explanation on how the algorithm works see AAGESEN *et al.* (2009).

Grid origin was arbitrarily defined and located at 70° long W and 22° lat S. We carried out the endemism analysis

Tab. I. Results of the endemicity analysis on data set from different taxa of small mammals (SM, small mammals; TSM, terrestrial small mammals; Ch, Chiroptera; Di, Didelphimorphia; Ro, Rodentia). The total number of consensus areas obtained by using different search (analytical) parameters (i.e., cell sizes and filling values; T) and the number of biogeographically informative areas (BI, or areas not almost equivalent to the study area, see main text) as a subset of the first are indicated. Cell sizes (in degrees) and filling values (first value: assumed presences, second value: inferred presences) are also indicated.

Taxa	SM		TSM		Di		Ch		Ro	
	T	BI	T	BI	T	BI	T	BI	T	BI
1°x1° 0-0	8	7	6	6	1	1	4	3	7	7
0.75°x0.75° 0-0	9	8	6	6	1	1	4	3	6	6
0.5°x0.5° 0-0	6	6	5	5	0	0	3	3	4	4
0.5°x0.5° 0-20	8	8	7	7	0	0	3	3	5	5
0.5°x0.5° 20-40	8	8	8	8	0	0	5	5	6	6
0.25°x0.25° 0-0	1	1	1	1	0	0	0	0	1	1
0.25°x0.25° 0-20	1	1	1	1	0	0	0	0	1	1
0.25°x0.25° 20-40	3	3	3	3	0	0	0	0	3	3
0.25°x0.25° 40-60	2	2	2	2	0	0	0	0	2	2
0.25°x0.25° 60-80	6	6	4	4	0	0	0	0	4	4
0.25°x0.25° 80-100	4	4	3	3	0	0	0	0	3	3
TOTAL	56	54	46	46	2	2	19	17	42	42

through a heuristic search and default NDM parameters: searching groups of cells by adding/eliminating one cell at a time, and saving groups defined by two or more endemic species and with scores higher or equal to 2.0. Groups of cells with more than 50% of species in common were ruled out retaining those with highest scores, and groups of cells with a score up to 1% inferior were stored in memory. We obtained consensus areas using the loose consensus rule in VNDM (see AAGESEN *et al.*, 2013).

The distributional patterns were evaluated in the context of traditional biogeographic divisions by plotting the distribution of the defining species upon the terrestrial eco-regions as defined by BURKART *et al.* (1999) and OLSON *et al.* (2001). The results were mapped using the program Global Mapper v11.02. Finally, all consensus areas were grouped in General Patterns (GPs) employing a qualitative criterion (see DASILVA *et al.*, 2015), according to their fit to the traditional biogeographic divisions considered.

RESULTS

We reviewed a total of 8,673 specimens, and we identified 8,400 of them to the species level. From these, 8,117 had precise punctual localities and represented 119 of the 124 NWA species included in this work (Appendix). Altogether, the principal database contains 11,596 geo-referenced records of 124 of the 128 known NWA small mammal species [exceptions are *Necomys amoenus* (Thomas, 1900), *Oxymycterus akodontius* Thomas, 1921, *Graomys edithae* Thomas, 1919, and *Ctenomys fochi* Thomas, 1919].

The results we obtained by analyzing data from the different taxa of small mammals are summarized in Tables I to IV. The analysis resulted in 165 consensus areas. Four large areas almost equivalent to the study region were not considered in the following characterization (see Discussion). The remaining 161 areas represent PDCs or AEs in strict sense characterized by 7 species of marsupials, 28 species of bats, and 63 species of rodents.

Thirty-two species (25% of all study region small mammal fauna that characterize consensus areas) are endemic to the study region and define six GPs that are AEs in strict sense (Tab. III). Other 12 GPs are mainly defined by widely distributed species (whose distributions exceed the study region) and therefore we consider these GPs as PDCs. Of all the 18 GPs, 6 (3 of the AEs in strict sense and 3 PDCs) run transversal to the Andes, in an east-west direction, and group together eastern and western Andean biomes, joining up lowland and moist or dry highland species (Figs 14-19). On the other hand, the other 9 PDCs run parallel to the Andes, in a north-south direction, including eastern or western Andean biomes (Figs 2-10). The other 3 AEs are located in the south of the study region, either on the eastern moist Andean slopes and lowlands or on the western dry valleys (Figs 11-13). Of the 18 GPs, 6 were previously identified (SANDOVAL & FERRO, 2014). The other 12 are novel distributional congruence patterns or are more detailed or precise definitions of some patterns previously outlined. Since the characterization of the GPs already reported by SANDOVAL & FERRO (2014) is basically the same, the new characterization is not included in the following statement. The number of areas equivalent to each of such GPs, the databases and cell sizes of the grids that allowed their identification, and the number, identity and distributional fit of the characterizing species are provided in Figs. 2-7, and in Tables II and III.

Local Patterns of Distributional Congruence

1. *Widespread Eastern Andean Slopes ("Argentinean Yungas")* (already obtained by SANDOVAL & FERRO, 2014; Fig. 2).
2. *North-eastern Andean Slopes ("Northern Argentinean Yungas")* (already obtained by SANDOVAL & FERRO, 2014; Fig. 3).
3. *A patch of the Northern Argentinean Yungas: Finca Las Capillas* (Fig. 4). Two consensus areas were equivalent to this pattern, which is nested within the *North-eastern*

- Andean Slopes* pattern. This PDC were only obtained analyzing the SM database with the smallest grid sizes (Tab. II). Three species characterize this PDC. There is one endemic species characterizing these areas (Tab. III).
4. *Eastern Andean Slopes and Lowlands* (“*Argentinean Yungas and Chaco*”) (Fig. 5). Two consensus areas were equivalent to this pattern. This PDC were obtained only analyzing the Ch database (Tab. II). Fifteen species characterize this PDC. There are none endemic species characterizing these areas (Tab. III).
 5. *North-eastern Andean Slopes and Lowlands* (“*Northern Argentinean Yungas and Chaco*”) (Fig. 6). Six consensus areas were equivalent to this pattern. This PDC were obtained analyzing the SM, TSM, and Ro databases with big grid sizes (Tab. II). Twenty-five species characterize this PDC. There are nine endemic species characterizing these areas (Tab. III).
 6. *Mountain Tops and Western Andean Slopes* (“*Northern Argentinean Highlands*”) (Fig. 7). Three consensus areas were equivalent to this pattern. This PDC were only obtained analyzing the TSM and Ro databases with large grid sizes (Table 2). Nine widely distributed species characterize this PDC (Tab. III).
 7. *Eastern Lowlands* (“*North-western Argentinean Chaco*”) (Fig. 8). Two consensus areas were equivalent to this pattern. This PDC were only obtained analyzing the TSM and Ro databases with the biggest grid sizes (Tab. II). Four widely distributed species characterize this PDC (Tab. III).
 8. *Widespread Western High Andes* (“*Puna*”) (already obtained by SANDOVAL & FERRO, 2014; Fig. 9).
 9. *North-western High Andes* (“*High Andes*”) (already obtained by SANDOVAL & FERRO, 2014; Fig. 10).
 10. *Eastern Andean Slopes merged with Western Andean Biomes (E-W): The combination of Argentinean Yungas, Chaco, and Monte* (Fig. 14). Two latitudinally extensive consensus areas were obtained in the study region (Tab. II). These areas were characterized by 23 species (Tab. III). Of these, 16 species correspond to the moist eastern slopes and lowlands, and 7 [*E. patagonicus* Thomas, 1924, *L. blossevillii* (Lesson & Garnot, 1826), *N. macrotis* (Gray, 1839), *S. lilium* (E. Geoffroy Saint-Hilaire, 1810), *C. tschudii* Fitzinger, 1857, *O. flavescens* (Waterhouse, 1837), and *P. osilae* J. A. Allen, 1901] inhabit both the western arid slopes and the eastern biomes.
 11. *North-eastern Andean Slopes merged with Northwestern Andean Biomes I (NE-NW): The combination of Argentinean Yungas and Puna* (Fig. 15). Three big consensus areas were obtained in the north of the study region (Tab. II). These areas were characterized by nine species (Tab. III). There are two endemic species (Tab. III). All characterizing species can be divided in two sets; a highland group of species [*A. albiventer* Thomas, 1897, *A. boliviensis* Meyen, 1833, *E. hirtipes* (Thomas, 1902), *E. puerulus* (Philippi, 1896), and *O. gliroides* (Gervais & d’Orbigny, 1844)] and a lowland or sylvan set [*A. budini* (Thomas, 1918), *M. keaysi* J. A. Allen, 1914, *O. paramensis* Thomas, 1902, and *T. wolffsohni* Thomas, 1902].
 12. *North-eastern Andean Slopes merged with North-western Andean Biomes II (NE-NW): A patch of High Andes, Puna, Monte, and Yungas in Jujuy province: Finca Las Capillas and nearby fragment of Sierra de Tilcara* (Fig. 16). Ten small consensus areas were obtained in the north of the study region (Tab. II). These areas were characterized by nine species (Tab. III). There are two endemic species (Tab. III). All characterizing species can be divided in two sets; a highland group of species [*A. jelskii* (Thomas, 1894), *A. sublimis* (Thomas, 1900), *C. budini* Thomas, 1913, *N. ebriosus* Thomas, 1894, and *P. caprinus* Pearson, 1958] and a lowland or sylvan set [*E. chiriquinus* Thomas, 1920, *H. velatus* (I. Geoffroy Saint-Hilaire, 1824), *M. rufus* E. Geoffroy Saint-Hilaire, 1805, and *T. primus* Anderson & Yates, 2000].
- Areas of Endemism
13. *South-eastern Andean Slopes* (“*Southern Argentinean Yungas*”) (already obtained by SANDOVAL & FERRO, 2014; Fig. 11).
 14. *South-eastern Andean Slopes and Lowlands* (“*Southern Argentinean Yungas and Chaco*”) (Fig.). Twenty-four consensus areas were equivalent to this pattern. This AE were obtained analyzing the SM, TSM, and Ro databases with small grid sizes (Tab. II). Eight species characterize this AE. There are six endemic species characterizing these areas (Tab. III).
 15. *South-western High Andes* (“*Monte Desert*”) (already obtained by SANDOVAL & FERRO, 2014; Fig. 13).
 16. *South-eastern Andean Slopes merged with South-western Andean Biomes I (SE-SW): The combination of Argentinean Yungas and Monte* (Fig. 17). Twelve consensus areas were equivalent to this GP. This AE was obtained analyzing the SM, TSM, and Ro databases with almost all grid sizes (except the biggest one). Ten species characterize this AE (Tab. III). Of these, three species correspond to the western arid slopes [*E. bolsonensis* Mares, Braun, Coyner & Van Den Bussche, 2008, *E. moreni* (Thomas, 1896), and *R. auritus* (G. Fischer, 1814)] and seven to the moist eastern slopes. There are nine endemic species.
 17. *South-eastern Andean Slopes merged with South-western Andean Biomes II (SE-SW): The combination of Argentinean Yungas, Chaco, and Monte* (Fig. 18). Ten consensus areas were equivalent to this GP. This AE was obtained analyzing the SM, TSM, and Ro databases with almost all grid sizes (except the smallest one). Nineteen species characterize this AE. Of these, four species correspond to the western arid slopes (*C. coludo* Thomas, 1920, *E. bolsonensis*, *E. moreni*, and *R. auritus*), 11 to the moist eastern slopes and lowlands, and four (*H. montanus*, *A. spagazzinii* Thomas, 1897, and *A. olrogi* Williams & Mares, 1978) inhabit both

the western arid slopes and the eastern biomes. There are 16 endemic species (Tab. III).

18. *South-eastern Andean Slopes merged with South-western Andean Biomes III (SE-SW): The combination of Argentinean Chaco and Monte* (Fig. 19). Three consensus areas were equivalent to this GP. This

AE was obtained analyzing the SM, TSM, and Ro databases with a moderate grid size. Three endemic species characterize this AE (Tab. III), of which one correspond to the western arid slopes (*P. aureus* Mares, Braun, Barquez, & Díaz, 2000) and the other two inhabit both the western arid slopes and the eastern lowlands.

Tab. II. Results of the endemicity analysis on data from different data set of small mammals. The number of consensus areas obtained by analyzing data from each of the taxa considered (S, small mammals; T, terrestrial small mammals; D, Didelphimorphia; C, Chiroptera, R, Rodentia) with grids with different cell sizes (a: 1°; b: 0.75°; c: 0.5°; d: 0.25°) is shown. Filling values are not shown. The General Pattern numbers (GP) correspond to those in the text.

	GP1					GP2					GP3					GP4					GP5					GP6				
	S	T	D	C	R	S	T	D	C	R	S	T	D	C	R	S	T	D	C	R	S	T	D	C	R	S	T	D	C	R
a	1	1	1	1	1					1										1	1	1				1	1			
b	1	2	1	1	2	1	1		1	1											1	1				1	1			
c	9	7		6	5	6	7		4	4										1										
d	1					2	1			1	1	1																		
To	12	10	2	8	8	9	9	0	6	6	1	0	0	0	0	0	0	0	0	0	2	0	2	2	0	0	2	0	2	0
			40					30					1					2					6						3	

	GP7					GP8					GP9					GP10					GP11					GP12				
	S	T	D	C	R	S	T	D	C	R	S	T	D	C	R	S	T	D	C	R	S	T	D	C	R	S	T	D	C	R
a		1					1	1															2							1
b							1	1							1					1										
c																														
d												1	1							1										
To	0	1	0	0	1	2	1	0	0	1	1	1	0	0	1	1	0	0	1	0	2	0	0	0	0	1	4	3	0	0
			2					4					3					2					3						10	

	GP13					GP14					GP15					GP16					GP17					GP18				
	S	T	D	C	R	S	T	D	C	R	S	T	D	C	R	S	T	D	C	R	S	T	D	C	R	S	T	D	C	R
a																					2	2								2
b																1	1				1	1								
c																1	2	2			2	1	1			1	1	1		
d	1	1				1	7	7			7					1	1				1									
To	1	1	0	0	1	8	8	0	0	8	1	1	0	0	1	4	4	0	0	4	4	3	0	0	3	1	1	0	0	1
			3					24					3					12					10						3	

Tab. III. Characterizing species of each biogeographically significant area obtained by analyzing data of different taxa under different search parameters (not shown). The numbers of the General Patterns (GP) correspond to those in the text. If the GP constitute a Local Pattern of Distributional Congruence (PDC) or an Area of Endemism in strict sense (AE) is specified. Restricted (R) and widely distributed (W) species of each GP are indicated.

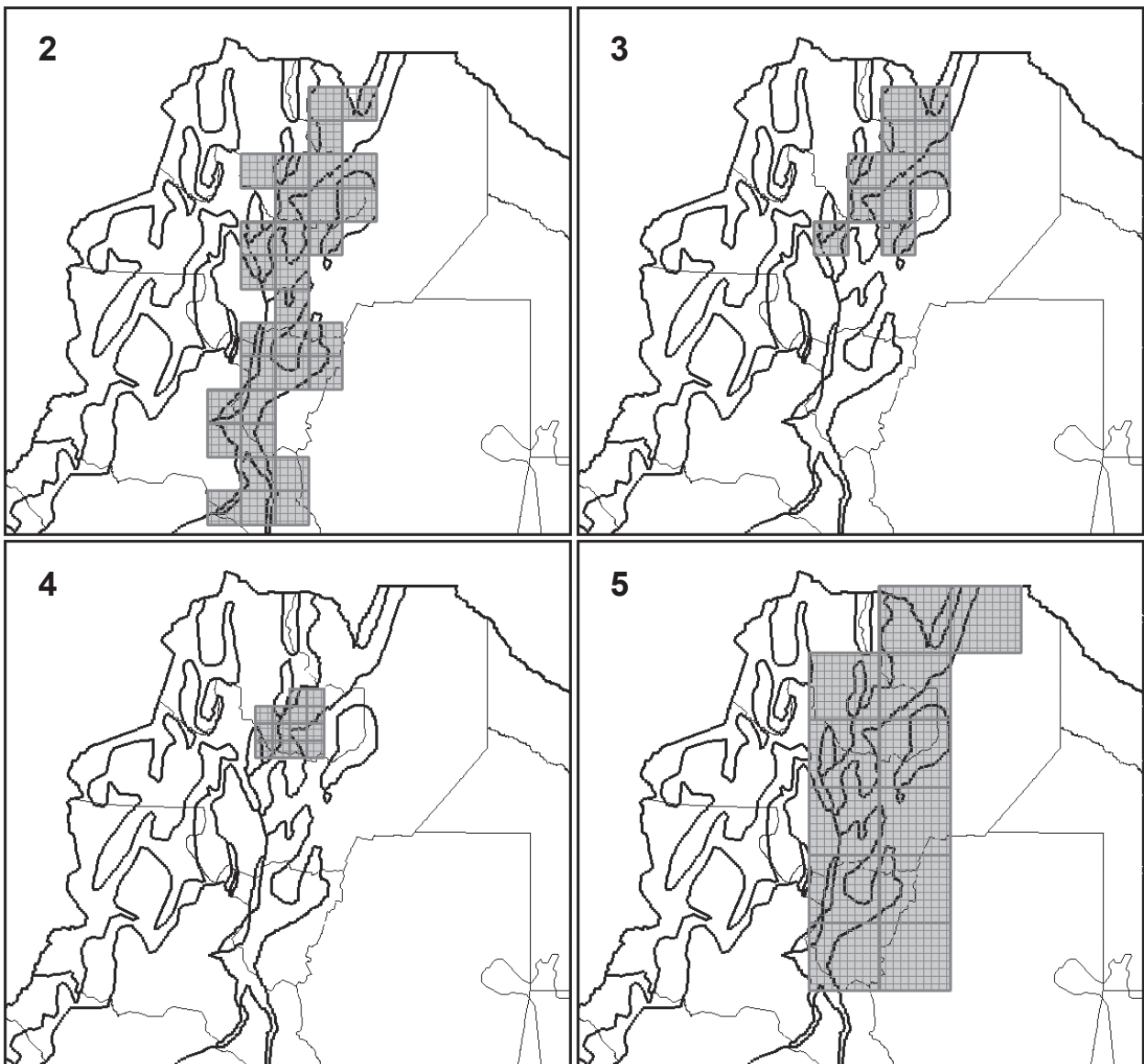
General Patterns	GP1	GP2	GP3	GP4	GP5	GP6	GP7	GP8	GP9	GP10	GP11	GP12	GP13	GP14	GP15	GP16	GP17	GP18	
Species	PDC	PDC	PDC	PDC	PDC	PDC	PDC	PDC	PDC	PDC	AE	AE	AE	PDC	PDC	PDC	AE	AE	AE
<i>Cryptonanus chacoensis</i>			W						W										
<i>C. ignitus</i>			R																
<i>Micoureus constantiae</i>	W					W													
<i>Thylamys cinderella</i>	R										R								
<i>T. pusillus</i>								W											
<i>T. sponsorius</i>	R										R								
<i>T. venustus</i>			W																
<i>Anoura caudifer</i>			W			W													
<i>A. planirostris</i>	W				W						W								
<i>Chrotopterus auritus</i>	W				W						W								
<i>Cynomops planirostris</i>			W			W													
<i>Diaemus youngi</i>			W			W													
<i>Eptesicus chiriquinus</i>			W		W								W						
<i>E. diminutus</i>	W				W						W								
<i>Eumops bonariensis</i>																			W
<i>E. glaucinus</i>	W				W	W					W								
<i>E. patagonicus</i>	W				W						W								
<i>Glossophaga soricina</i>			W			W													
<i>Histiotus laephotis</i>	W				W						W								
<i>H. macrotus</i>									W										
<i>H. montanus</i>																			W

Tab. III. Cont.

General Patterns	GP1	GP2	GP3	GP4	GP5	GP6	GP7	GP8	GP9	GP10	GP11	GP12	GP13	GP14	GP15	GP16	GP17	GP18
Species	PDC	PDC	PDC	PDC	PDC	PDC	PDC	PDC	PDC	AE	AE	AE	PDC	PDC	PDC	AE	AE	AE
<i>H. velatus</i>		W	W									W						
<i>Lasiurus blossevillii</i>	W			W						W								
<i>Myotis microtis</i>		W			W													
<i>M. rufus</i>		W			W									W				
<i>M. albescens</i>	W			W						W								
<i>M. keaysi</i>	W			W							W							
<i>M. riparius</i>	W			W						W								
<i>Noctilio leporinus</i>	W				W													
<i>Nyctinomops laticaudatus</i>	W			W	W					W								
<i>N. macrotis</i>	W			W						W								
<i>Pygoderma bilabiatum</i>		W			W													
<i>Sturnira erythromos</i>	W			W						W								
<i>S. lilium</i>	W			W						W								
<i>S. oporaphilum</i>	W			W						W								
<i>Abrothrix andinus</i>						W		W										
<i>A. illuteus</i>																	R	R
<i>A. jelskii</i>									W			W						
<i>Akodon albiventer</i>								W			W							
<i>A. aliquantulus</i>														R				
<i>A. boliviensis</i>		W			W						W							
<i>A. budini</i>		R			R						R							
<i>A. caenosus</i>	W									W								
<i>A. fumeus</i>		R			R													
<i>A. simulator</i>	W																	
<i>A. spegazzinii</i>	W																	R
<i>A. sylvanus</i>		R			R													
<i>A. toba</i>					W													
<i>Andalgalomys olrogi</i>																		R
<i>Andinomys edax</i>	W					W												
<i>Auliscomys sublimis</i>									W			W						
<i>Bolomys lactens</i>	R									R								
<i>B. lenguarum</i>	W																	
<i>Calomys callosus</i>								W										
<i>C. lepidus</i>	W					W												
<i>C. musculus</i>							W											
<i>Cavia tschudii</i>	W									W								
<i>Ctenomys budini</i>									R			R						
<i>C. coludo</i>															R		R	R
<i>C. knighti</i>																	R	R
<i>C. latro</i>														R			R	R
<i>C. occultus</i>																	R	R
<i>C. opimus</i>						W		W										

Tab. IV. Minimum and maximum endemicity values and supporting species for each General Pattern (GP). The numbers of the GPs correspond to those in the text.

	Minimum endemicity value	Maximum endemicity value	Number of supporting species
GP1	2.04	19.41	36
GP2	2.14	10.98	23
GP3	2.34	2.34	3
GP4	4.28	9.25	15
GP5	2.99	14.52	25
GP6	3.06	3.77	9
GP7	2.06	2.57	4
GP8	2.26	2.59	6
GP9	4.09	4.09	5
GP13	2.45	2.45	4
GP14	2.06	2.84	8
GP15	2.05	2.05	3
GP10	8.34	11.85	23
GP11	2.74	3.86	9
GP12	2.2	4.98	9
GP16	2.17	5.22	10
GP17	2.22	6.29	19
GP18	2.11	2.11	3



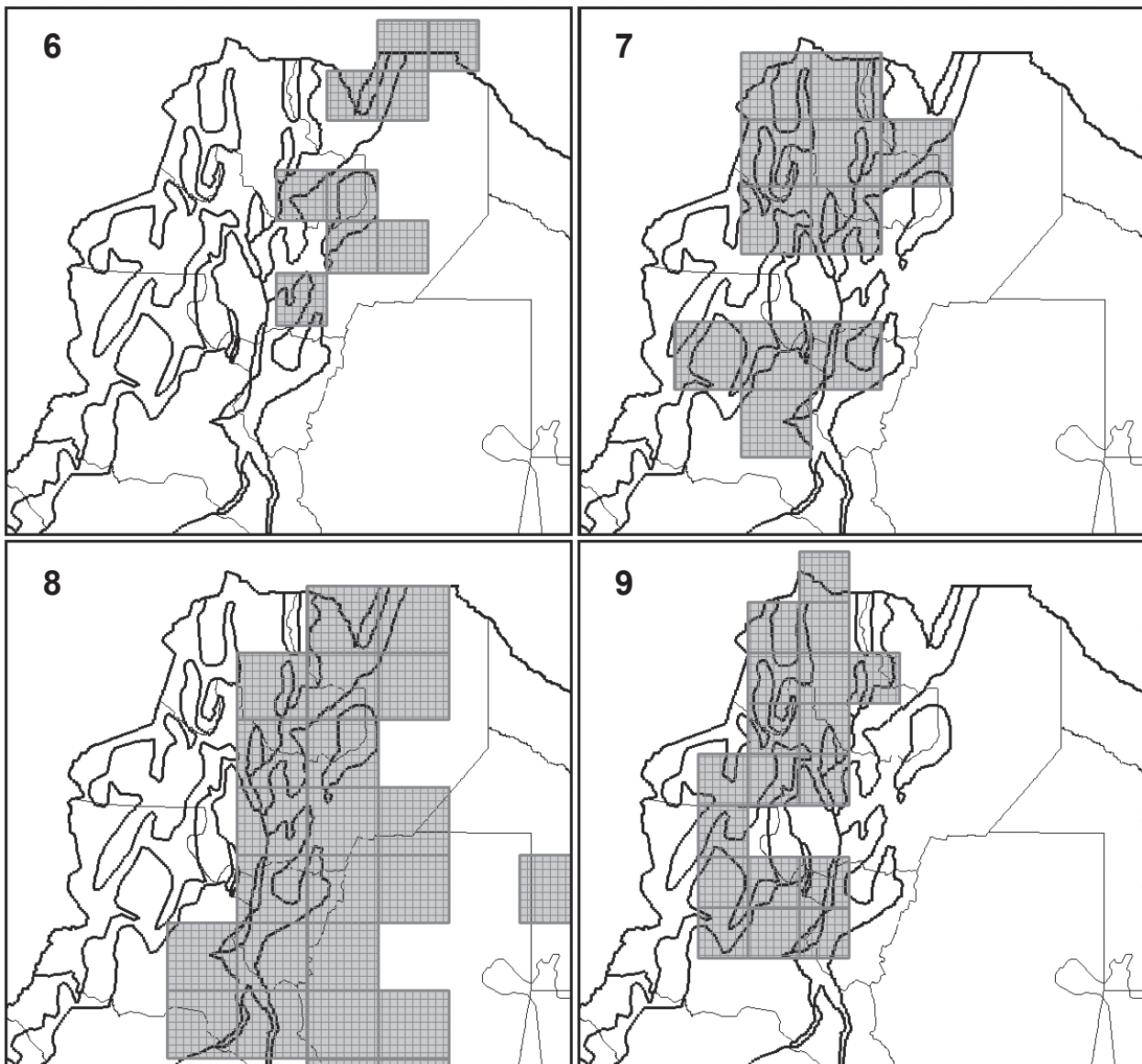
Figs 2-5. Fig. 2, a case of GP1, *Widespread Eastern Andean Slopes* PDC recovered through the analysis of SM database and with a grid of cells of $0.5^{\circ} \times 0.5^{\circ}$ and filling values of 0 for assumed presences and 20 for inferred presences. Fig. 3, a case of GP2, *North-eastern Andean Slopes* PDC recovered through the analysis of TSM database and with a grid of cells of $0.5^{\circ} \times 0.5^{\circ}$ and filling values of 0 for assumed presences and 20 for inferred presences. Fig. 4, a case of GP3, *A patch of the Northern Argentinean Yungas: Finca Las Capillas* PDC recovered through the analysis of SM database, with a grid of cells of $0.25^{\circ} \times 0.25^{\circ}$ and filling values of 80 for assumed presences and 100 for inferred presences. Fig. 5, a case of GP4, *Eastern Andean Slopes and Lowlands* PDC recovered through the analysis of Ch database, with a grid of cells of $1^{\circ} \times 1^{\circ}$ and without filling values.

DISCUSSION

Floristic vs faunal patterns. As highlighted by GODOY-BÜRKI *et al.* (2013), since endemism is a fundamental criterion to identify conservation areas, it is urgent that botanists and zoologists to conduct local distributional analyses, “in order to obtain an integrated solution for protecting both the flora and fauna in the region” (GODOY-BÜRKI *et al.*, 2013). In fact, in NWA there are hotspots for vascular plants and several animal taxa, including mammals (SZUMIK *et al.*, 2012). However, knowledge on distributional patterns and endemism for this region is very uneven among different taxa.

Surprisingly, it seems that, while detailed

quantitative analyses of plant species distribution data do not result in units that correspond to Cabrera’s phytogeographic divisions at this spatial scale (AAGESEN *et al.*, 2012), analyses of animal (here, small mammal) species distribution data generally do. So, despite the system Cabrera used was not based on quantitative studies and did not apply consistent criteria for defining the individual phytogeographic units (AAGESEN *et al.*, 2012), what he observed in local and regional flora composition may be determining animal distributions (e.g. SANDOVAL *et al.*, 2010; SZUMIK *et al.*, 2012; SANDOVAL & FERRO, 2014), although plant endemic species distribution quantitative analyses result in areas of endemism that do not correspond to his divisions (AAGESEN *et al.*, 2012). Although many of

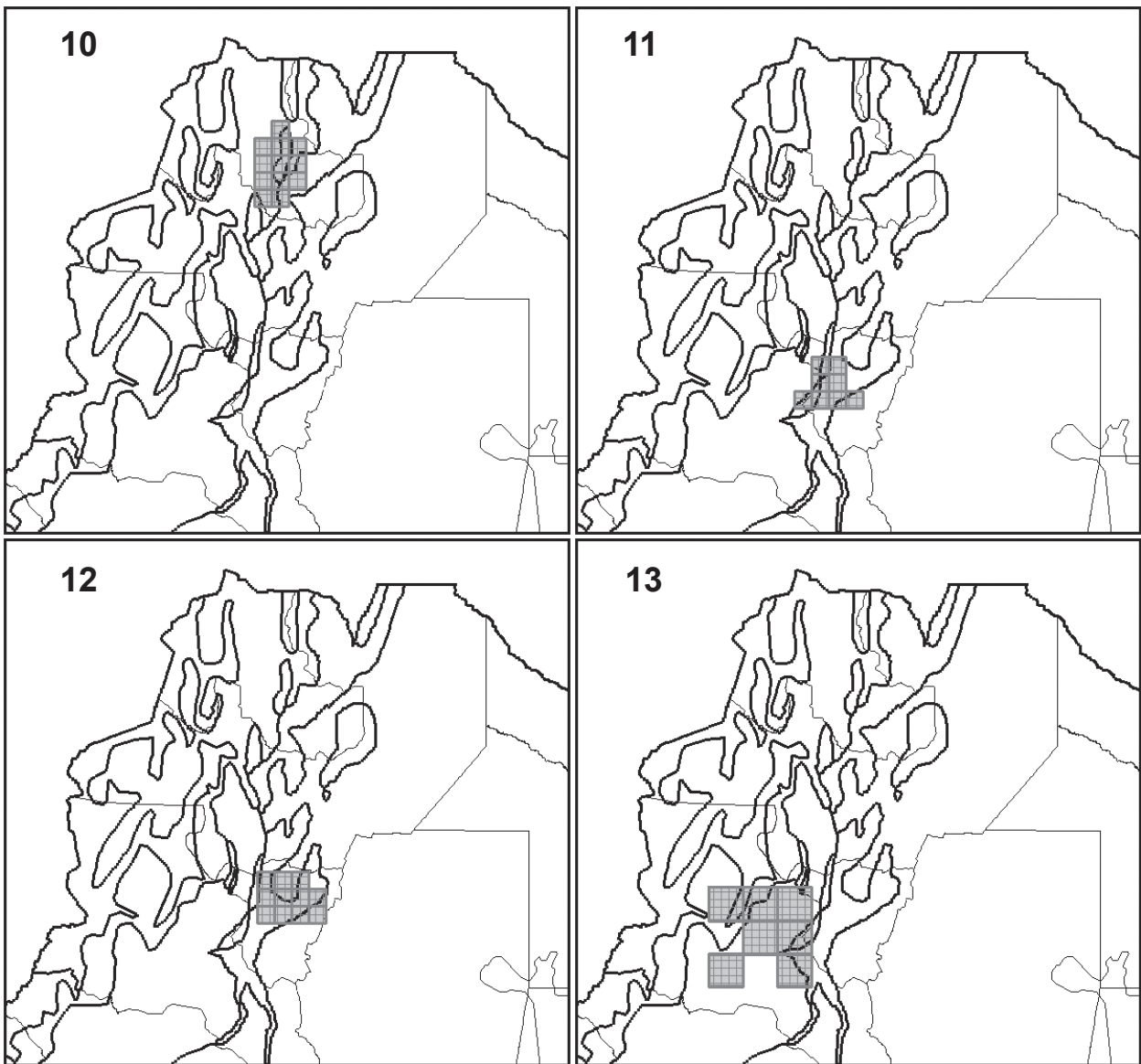


Figs 6-9. Fig. 6, a case of GP5, *North-eastern Andean Slopes and Lowlands* PDC recovered through the analysis of TSM database, with a grid of cells of $0.75^{\circ} \times 0.75^{\circ}$ and without filling values. Fig. 7, a case of GP6, *Mountains Tops and Western Andean Slopes* PDC recovered through the analysis of TSM and Ro databases, with a grid of cells of $1^{\circ} \times 1^{\circ}$ and without filling values. Fig. 8, a case of GP7, *Eastern Lowlands* PDC recovered through the analysis of TSM database, with a grid of cells of $1^{\circ} \times 1^{\circ}$ and without filling values. Fig. 9, a case of GP8, *Widespread Western High Andes* PDC recovered through the analysis of SM, TSM, and Ro databases, with a grid of cells of $0.75^{\circ} \times 0.75^{\circ}$ and without filling values.

the areas we obtained, both AEs and PDCs, are constituted by cells that include a wide array of habitats, the natural history and habitat preferences of the characterizing species allow us to certainly relate them to phytogeographic units previously defined by Cabrera (CABRERA & WILLINK, 1973; CABRERA, 1976).

All the obtained AEs are located in the south of the study region, either in the eastern Andean slopes and the western Andean biomes, and even in many cases those landscapes are merged in one AE. Similarly to what happens with vascular plants (AAGESEN *et al.*, 2012), small mammal endemic species are far from evenly distributed in the study region. Of the 33 endemic species (Table 3), only five are more or less latitudinally widely distributed [*T. cinderella* (Thomas, 1902), *T. sponsorius* (Thomas, 1902), *B. lactens*

(Thomas, 1918), *G. domorum* (Thomas, 1902), and *M. shiptoni* (Thomas, 1925)]. Interestingly, endemism, unlike what happens in vascular plants (AAGESEN *et al.*, 2012), does not declines towards the south, but does declines towards the west of the study region. Ten endemic species have their distributional ranges located in the north of the study region meanwhile 18 are in the south of the study region. On the other hand, 23 species inhabit in environments of eastern Andean slopes and lowlands meanwhile only ten inhabit western Andean biomes. The geographical location of our AEs and PDCs are mostly congruent with the most important hotspots for endemic vascular plant species. Our largest GPs include almost all the endemic species hotspots defined by GODOY-BÜRKI *et al.* (2013). And there are even coincidences at a more local scale: our GP16

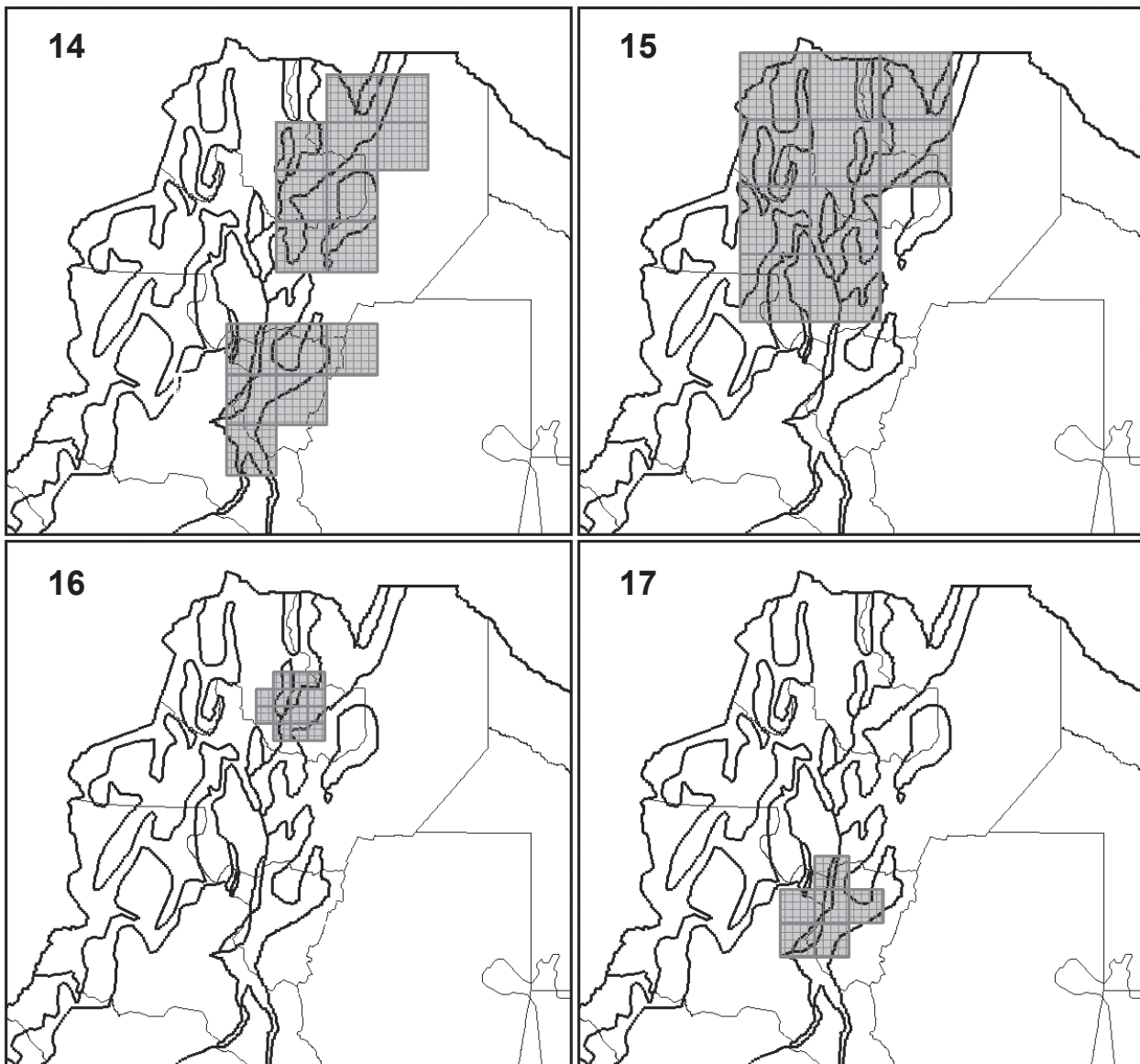


Figs. 10-13. Fig. 10, a case of GP9, *North-western High Andes* PDC recovered through the analysis of SM, TSM, and Ro databases, with a grid of cells of $0.25^{\circ} \times 0.25^{\circ}$ and filling values of 80 for assumed presences and 100 for inferred presences. Fig. 11, a case of GP13, *South-eastern Andean Slopes* AE recovered through the analysis of SM, TSM, and Ro databases, with a grid of cells of $0.25^{\circ} \times 0.25^{\circ}$ and filling values of 20 for assumed presences and 40 for inferred presences. Fig. 12, a case of GP14, *South-eastern Andean Slopes and Lowlands* AE recovered through the analysis of SM, Ch, and Ro databases, with a grid of cells of $0.25^{\circ} \times 0.25^{\circ}$ and filling values of 60 for assumed presences and 80 for inferred presences. Fig. 13, a case of GP15, *South-western High Andes* AE recovered through the analysis of SM, TSM, and Ro databases, with a grid of cells of $0.5^{\circ} \times 0.5^{\circ}$ and filling values of 0 for assumed presences and 20 for inferred presences.

(Fig. 17) includes the Sierra del Aconquija, between the provinces of Tucumán, Salta and Catamarca, which has the highest concentration of endemic plant species in the study region (GODOY-BÜRKI *et al.*, 2013); and our GP15 (Fig. 13), which includes Andalgalá, Santa María, and Ambato in Catamarca, was recognized as another important AE for plant endemism (GODOY-BÜRKI *et al.*, 2013).

Endemism and co-occurrence patterns. Highest numbers of endemic species (but not necessarily recognized AEs) are found in the eastern Andean slopes in Jujuy and Tucumán/Catamarca, with nine and eight endemic species respectively, and in the western Andean biomes in Tucumán/Catamarca, with eight endemic species. Of these three high

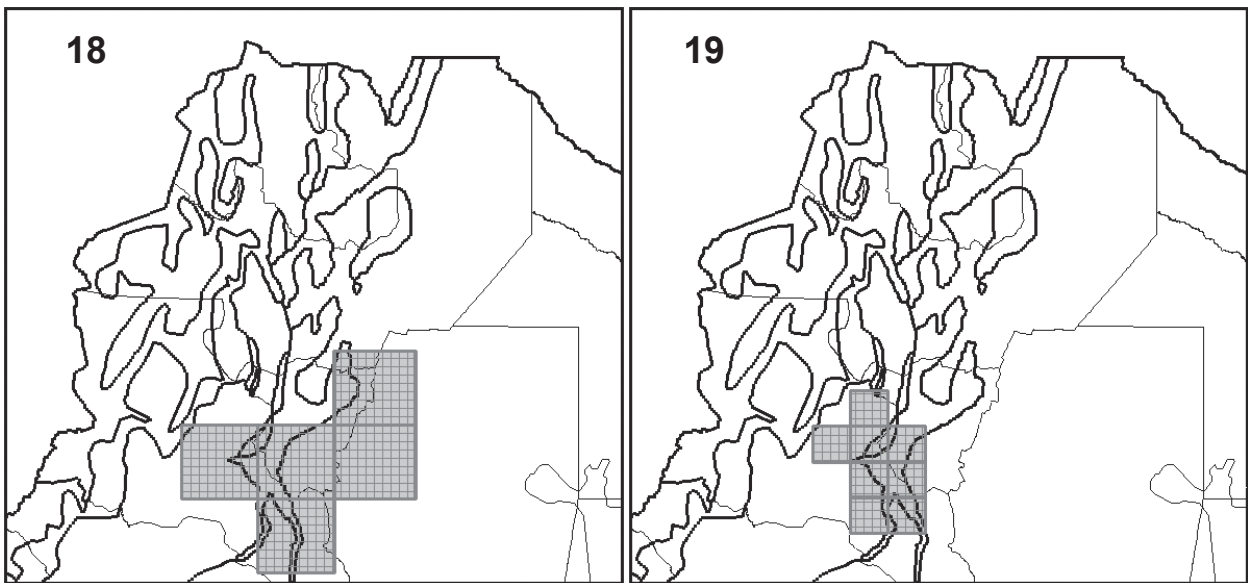
endemism sites that we *a priori* and qualitatively identified, our analysis was able to recover two patterns as AEs in strict sense, while the other was recovered as PDCs (which are characterized both by endemic and non-endemic species). However, both endemism patterns are impoverished in term of defining species: in any case the recovered areas were characterized by the complete assemblage of endemic species but only by a subset of such species (Tab. III). The *South-eastern Andean Slopes* pattern is an AE and corresponds to an endemism peak. SANDOVAL & FERRO (2014) recovered this pattern, characterized by 14 rodent species, 12 been endemic to the study region, been our GP also characterized only by rodent species (but far fewer).



Figs 14-17. Fig. 14, a case of GP10, *Eastern Andean Slopes merged with Western Andean Biomes (E-W)* PDC recovered through the analysis of SM and Ch databases, with a grid of cells of $0.75^{\circ} \times 0.75^{\circ}$ and without filling values. Fig. 15, a case of GP11, *North-eastern Andean Slopes merged with Northwestern Andean Biomes I (NE-NW)* PDC recovered through the analysis of SM database, with a grid of cells of $1^{\circ} \times 1^{\circ}$ and without filling values. Fig. 16, a case of GP12, *North-eastern Andean Slopes merged with North-western Andean Biomes II (NE-NW)* PDC recovered through the analysis of SM, TSM, and Ro databases, with a grid of cells of $0.25^{\circ} \times 0.25^{\circ}$ and filling values of 20, 40, and 60 for assumed presences and 40, 60, and 80 for inferred presences. Fig. 17, a case of GP16, *South-eastern Andean Slopes merged with South-western Andean Biomes I (SE-SW)* PDC recovered through the analysis of SM, TSM, and Ro databases, with a grid of cells of $0.5^{\circ} \times 0.5^{\circ}$ and without filling values.

Despite the low number of our characterizing species, this AE has a high endemism score and repeated occurrence (Tab. IV). This pattern corresponds to the Southern sector of the Yungas forest of NWA, which has been differentiated by phytogeographers as an impoverished version of the Northern sector rather than on exclusive floral elements (CABRERA, 1976; MORALES, 1996; BROWN *et al.*, 2001). Moreover, AAGESEN *et al.* (2012) reported that vascular flora endemism declines gradually towards the south of the study region. However, this area was recovered for insects (NAVARRO *et al.*, 2009), for a taxonomically diverse data set when analysed using quantitative approaches (SZUMIK *et al.*, 2012), and for rodents (SANDOVAL & FERRO, 2014; our

study), revealing the Southern sector of the Argentinean Yungas as a distinctive faunal AE, and, at least in the case of endemic small mammals, not a impoverished one. On the other hand, regarding the case of the other obtained AE that corresponds to an endemism peak, the Monte biogeographic province in NWA was recovered as and named as the *South-western High Andes* pattern. This western Andean biome occurs on the arid western (rain shadow) slopes. As the Yungas forest reach its southern tip on the humid eastern Andean slopes in NWA, the Monte province reaches its northernmost extension on the west-faced slopes of the same mountain ranges. Also, one of the highest concentrations of endemic plant species were found mostly



Figs 18, 19. Fig. 18, a case of GP17, *South-eastern Andean Slopes merged with South-western Andean Biomes II (SE-SW)* PDC recovered through the analysis of SM database, with a grid of cells of $1^{\circ} \times 1^{\circ}$ and without filling values (Southern area; see Results). Fig. 19, a case of GP18, *South-eastern Andean Slopes merged with South-western Andean Biomes III (SE-SW)* PDC recovered through the analysis of SM, TSM, and Ro databases, with a grid of cells of $0.5^{\circ} \times 0.5^{\circ}$ and filling values of 20 for assumed presences and 40 for inferred presences.

in the High Monte environments, especially in transition zones with the Southern Andean Yungas (GODOY-BÜRKI *et al.*, 2013).

Unlike to what happens with endemic vascular plants (AAGESEN *et al.*, 2012; GODOY-BÜRKI *et al.*, 2013), whose hotspots at a regional scale are concentrated in the arid ecoregions of NOA (with 80% of the endemic flora; AAGESEN *et al.*, 2012), the principal habitat types for endemic small mammal species are not the western or eastern arid or semi-arid biomes, but the eastern humid Andean slopes, with 20 endemic species (*versus* 13 in arid and semi-arid environments). Notwithstanding, arid/semi-arid biomes and humid landscapes are represented by the same number of AEs: one for arid/semi-arid biomes (GP15), one for humid landscapes (GP13), and four mixed GPs, which include both habitat types (GP14, 16, 17, and 18). Contrary to our results, AAGESEN *et al.* (2012) reported that very few vascular plant species are restricted to subhumid or humid environments in this region. They highlighted this surprising poverty in endemic species of the otherwise diverse Tucumano-Bolivian Yungas forest at a local scale. It should be noted that AAGESEN *et al.* (2012) stressed that the mountain grasslands above the tree line were included in the Puna (following IBISCH *et al.*, 2003), meanwhile in the phytogeographical scheme outlined by CABRERA (1976), which we follow, these grasslands are considered the highest strata of the Yungas. Notoriously, supporting IBISCH *et al.* (2003) scheme, we obtained the *Mountain Tops and Western Andean Slopes* pattern (a PDC), which, even though it represents an association between areas, apparently not correspond to a transition zone between biogeographic units but a natural unit characterized by species mostly inhabiting all environments represented in the area. Obtaining this GP allows formally grouping all those highlands environments

(High Andes, Puna, and mountain grasslands) that harbour common assemblages of rodent species. This issue will be presented in more detail in another manuscript. On the other hand, the *Widespread Eastern Andean Slopes* allows us to identify the entire latitudinal extension of the Yungas forest as a discrete biogeographic unit regarding the NWA geographic context. This is a stable pattern since it was recovered with different databases with different grid sizes (Tab. II). However, only 5 of the 36 species that characterize the Yungas forest are exclusive or almost exclusive of the NW Argentinean Yungas. This may well indicate that the Yungas of NWA may be part of a larger AE extending beyond the limits of our study region: the Yungas forest in NWA is the tail of a broader area that extends towards the north through Bolivian Yungas and probably to southern Peru. Alternatively, the recognition of distributional congruence in the species distributions may be due to a similar response to a unique combination of ecological and historical factors restricting species ranges that not necessarily affect in the same way these species north or southwards. The recognition of this pattern was also reported for bats and marsupials (SANDOVAL *et al.*, 2010) and for rodents (SANDOVAL & FERRO, 2014). Meanwhile, the *North-eastern Andean Slopes*, near the Bolivian border, is just traversed by the Tropic of Capricorn. Certainly, the northern part is the richest sector of the NWA Yungas forest which gradually impoverished southward (OJEDA & MARES, 1989; OJEDA *et al.*, 2008), although this statement do not applies to endemic small mammal species (see above). For bats and marsupials (SANDOVAL *et al.*, 2010) and for rodents (SANDOVAL & FERRO, 2014) the Northern sector of the Argentinean Yungas was also recovered. Contrary to the low number of endemic species found by SANDOVAL & FERRO (2014) for this pattern, according to our

results, almost half of the defining species (9 of the 23) are exclusive or almost exclusive to this PDC. Notably, even defined as a PDC, the fact of containing several endemic species would not allow a delimitation of an AE in the context the analyses we performed. Probably, this PDC would be obtained as an AE if distributional records of only endemic species are included in a study that do not include widespread species (AAGESEN *et al.*, 2012). In that case, perhaps we could define a PDC and an overlapping AE, and they would belong to the same GP. However, given that our analyses include both endemic and widely distributed species in the datasets, we can only speculate.

We identify Argentinean High Andes (*North-western High Andes*, GP9) and Puna (*Widespread Western High Andes*) provinces as discrete biogeographic units in the geographic context of NWA. Maybe, the High Andes and the Puna of NWA are part of larger AEs extending southward in Argentina and northward into Bolivia. For rodents (SANDOVAL & FERRO, 2014) the Argentinean High Andes and Puna were also recovered. However, as for vascular plants, the relative low number of endemic highland species is unexpected and may be underestimated as collection localities in those landscapes are scarce (AAGESEN *et al.*, 2012). As SANDOVAL & FERRO (2014) mentioned, large areas of these highlands remain unexplored and so further exploration should clarify the existence of different AEs associated with mountaintops on the highlands of NWA. Despite that, one of the highest concentrations of endemic plant species were found mostly in the Central Andean Puna environments, especially in transition zones with the Southern Andean Yungas (GODOY-BÜRKI *et al.*, 2013).

SZUMIK *et al.* (2012) were able to recover the Chaco biogeographic province but later SANDOVAL & FERRO (2014) failed to recognize it neither as an AE nor as a PDC. We recovered the Chacoan biome both as hybrid areas, mixed with the Yungas environments (the *Eastern Andean Slopes and Lowlands* and the nested *North-eastern Andean Slopes and Lowlands* and *South-eastern Andean Slopes and Lowlands*) and as independent areas (*Eastern Lowlands*, GP7). Although the scattered sampling localities may prevent or difficult its identification as a sympatric distributional pattern, the Chacoan small mammals, and the species inhabiting both biomes (Chaco and Yungas), allow the recognition of this biogeographic province as a PDC (see also SANDOVAL & BARQUEZ (2013) for a detailed interpretation of the Chacoan bat fauna assemblages).

Finally, despite the identification of four large areas almost equivalent to the study region, we were not able to obtain a pattern equivalent to the southern part of the central Andes, which was recognized as a single AE, defined by at least 53 species of vascular plants that are widely distributed within the study region but are endemic to it (AAGESEN *et al.*, 2012). We considered our four wider consensus areas biogeographically not informative at this spatial scale because they have a too large surface (as mentioned, almost equivalent to the study region) and are characterized by many widespread species, in some

cases presenting high endemicity values, all these making impossible their interpretation at this analysis scale. In our spatial scale of analysis, these areas could be interpreted as areas that integrate transition zones, because they present varied and complex characterizing faunas. So, it is likely that these areas are part of a more inclusive pattern evident to a larger scale of analysis. However, this interpretation is purely speculative. For these reasons, those areas are not considered in this discussion.

‘Spurious’ areas? Finally, we obtained three sets of ‘merged-unit’ areas: latitudinally extensive (GP10) and northern (GP11 and 12) and southern (GP16, 17, and 18) groupings of eastern and western Andean biomes. All these areas combine consensus areas corresponding to well defined classic main patterns. SANDOVAL & FERRO (2014) interpreted these areas as ‘spurious’ areas and, as AAGESEN *et al.* (2013) stated, as a likely outcome of using the ‘loose’ consensus rule. The loose rule merges areas if they share a user defined percentage of their defining species with at least one other area in the consensus (AAGESEN *et al.*, 2013). The ‘loose’ consensus rule is a useful tool for detecting gradual overlapping distribution patterns and replacement among areas. Therefore, SANDOVAL & FERRO (2014) considered that the spurious areas may well be indicating a transition zone between the main patterns involved. Some of our ‘merged-unit’ areas actually seem to be what SANDOVAL & FERRO (2014) called ‘spurious’ areas, since they more likely represent turnover gradients rather than congruence patterns (Augusto Ferrari, com. pers.). Interestingly, AAGESEN *et al.* (2012) do not share our view. In their analyses all areas were characterized by species from very different altitudes that do not necessarily strictly coexist but are founded in the same cell or cell set because in the study region several phytogeographic units are separated from each other by very short distances. They consider those AEs as valid and their high endemic areas include several environments and are characterized by vascular plant species that are not sympatric but inhabit highly altitude and aridity variable landscapes. This is the case of GP11, 12 (both PDC), and 16 (an AE), because in these areas species that are not sympatric at all, which inhabits very environmentally different landscapes, are grouped.

However, GP10 (a PDC), 17, and 18 (both AEs) include some species that are in fact sympatric. Moreover, these areas are among the high endemic areas found when analyzing the endemic vascular flora (AAGESEN *et al.*, 2012) and present high concentrations of endemic plant species (especially the transition zones from the Southern Andean Yungas to the High Monte, GODOY-BÜRKI *et al.*, 2013). So, interestingly, small mammals and vascular plants appear to define the same AEs in NWA (Lone Aagesen, com. pers.). This finding is very important, especially considering that areas with high levels of endemism are priorities for conservation because they reflect past and potentially future speciation events (ROSENZWEIG, 1995; FA & FUNK, 2007). Therefore, areas identified by their high number of endemic

taxa represent essential conservation targets particularly if occurring in rather small geographic areas (VANE-WRIGHT *et al.*, 1991; LINDER, 1995; PETERSON & WATSON, 1998).

Taxa. Rodent species define 15 of the 18 GPs, while bats define four and marsupials only define one. The GP defined by bats and marsupials and two defined by bats are also defined by rodents. So, only three GPs are not recovered through the analysis of rodent species distributional data, and even these GPs have rodent characterizing species when analyzed together with all small mammal species (GP3 and GP10). Only in GP4 rodents have no participation at all. Clearly, at this spatial scale, non-flying mammals, particularly rodents, are biogeographically more valuable species than flying mammals (bat species). The other terrestrial small mammals considered (marsupials) include very few (10) and not always distributionally overlapping species in NWA, and this is probably why they are so little involved in the characterization of areas, compared to rodents. Therefore, as suggested by SANDOVAL & FERRO (2014), rodents are very useful to analyse patterns of endemism and biogeographical regionalization in small geographical areas. This is probably due to the fact that a large proportion of mammals with restricted distributions are rodents, independently of their taxonomic level (genera/species) or spatial scale (ARITA *et al.*, 1997; DANELL, 1999; DANELL & AAVA-OLSSON, 2002), that they are present in all type of biomes from tropical moist forest to gelid highland deserts, and that they constitute quite conspicuous assemblages as a consequence of adaptation to environments (MENA & VÁZQUEZ-DOMÍNGUEZ, 2005; PATTERSON *et al.*, 1998). Moreover, rodents are the most diverse order of mammals containing 42% of known species (MUSSER & CARLETON, 2005), thus frequently being the most important part of mammal assemblages concerning number of species.

Using different search (analytical) parameters.

Numerous studies support the hypothesis that the results obtained at a given spatial or temporal scale can not necessarily be obtained or be significant at larger or smaller scales (LYONS & WILLIG, 1999, and references cited therein), so it is interesting and valuable to document scale dependence of different patterns. CASAGRANDE *et al.* (2009) analyzed the implications of using different scales of analysis with the optimality method, recovering some patterns at all spatial scales, but also recovering certain patterns only in some particular scale. According to LAFFAN & CRISP (2003), we are closer to finding a complete representation of the true pattern of distributional congruence and endemism varying the spatial scale of analysis than without doing it. In our analysis, the dependence of local patterns of distributional congruence and endemism on the spatial scale does not seem to be decisive: most patterns remain constant during the analysis at different scales (i.e., grid sizes). Our GP1 and 2 are obtained using four different grid sizes, GP16 and 17 are obtained using three different grid sizes, and GP4, 5, 6, 8, 12, and 14 are obtained using two different grid sizes (Tab. II). Distributional congruence

and endemism patterns that do not support changes in the cell size can be a simple artifact of a specific grid, while resistance to changes in cell size is an important factor in assessing a particular distributional pattern (AAGESEN *et al.*, 2009). According to this framework, our GP3, 7, 9, 10, 11, 13, 15, and 18 could be artifacts of the technique without a real biogeographical significance. Considering this, we think that in fact recognition of GP3 (*A patch of the Northern Argentinean Yungas: Finca Las Capillas*), which constitutes a nested area within the Northern sector of the Argentinean Yungas, may be due to the substantial sampling effort invested in this area by Dr. Barquez and its working group: the area was visited on numerous occasions, in different seasons, the last almost 20 years. Thus, this small area of the Argentinean Yungas might be seen as a sampling artifact rather than isolated populations inhabiting only there in Argentina. Further exploration around this area should clarify whether the disjunction of the distribution of the characterizing species is real, or if this area is part a continuous area extending northward. However, as highlighted by AAGESEN *et al.* (2012), in some instances, dependence on obtaining a pattern to a particular grid cell size, may relate to the characteristics of the available data and not necessarily with the validity of the pattern, since small cell sizes requires collection sites are very close to each other. In the cases that collection sites are not so closely, the pattern will emerge only when using larger cell sizes which allow wider distances between the collection sites (AAGESEN *et al.*, 2012). We think this is the case of GP7, 9, 13, and 15. General Patterns 13 (*South-eastern Andean Slopes*) and 15 (*South-western High Andes*), which constitute AEs in strict sense, was already discussed (see above).

CONCLUSIONS

While detailed quantitative analysis of plant species distribution data does not result in units that correspond to Cabrera's phytogeographic divisions at this spatial scale, analysis of animal species distribution data does. Even in a region whose biogeographical patterns have been studied based on several of its floral and faunal species, we were able to identify previously unknown meaningful faunal patterns (*Eastern Andean Slopes and Lowlands, North-eastern Andean Slopes and Lowlands, South-eastern Andean Slopes and Lowlands, Eastern Lowlands, and Mountain Tops and Western Andean Slopes*) and more accurately define some of those already identified. We identify PDCs and AEs that conform Eastern Andean Slopes Patterns, Western High Andes Patterns, and Merged Eastern and Western Andean Slopes Patterns, some of which are re-interpreted at the light of known patterns of the endemic vascular flora. Endemism do not declines towards the south, but do declines towards the west of the study region. Highest numbers of endemic species (but not necessarily recognized AEs) are found in the eastern Andean slopes in Jujuy and Tucumán/Catamarca, and in the western Andean

biomes in Tucumán/Catamarca. The principal habitat types for endemic small mammal species are the eastern humid Andean slopes. Notwithstanding, arid/semi-arid biomes and humid landscapes are represented by the same number of AEs. Rodent species define 15 of the 18 GPs, and only in one they have no participation at all. Clearly, at this spatial scale, non-flying mammals, particularly rodents, are biogeographically more valuable species than flying mammals (bat species).

Acknowledgments. MLS thanks David Flores (Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires), Ricardo Ojeda (Instituto Argentino de Investigaciones de Zonas Áridas, Mendoza), Ulyses Pardiñas (Centro Nacional Patagónico, Puerto Madryn, Chubut), Diego Verzi (Museo de La Plata, La Plata, Buenos Aires), Sergio Bogan (CFA), and Damián Romero (Museo Municipal de Ciencias Naturales “Lorenzo Scaglia”, Mar del Plata, Buenos Aires) for access to the small mammal specimens under their care. MLS wants to thank CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas, National Council of Scientific and Technical Research), for her doctoral fellowships. We all thank Lone Aagesen for her comments and suggestions, which greatly helped us to improve the original manuscript, and Carlos Iudica for his kind review of the writing our manuscript.

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Appendix. Small mammals species included in the analysis. The taxonomy used herein mainly follows that outlined in WILSON & REEDER (2005) and BARQUEZ *et al.* (2006). For details on the taxonomic criteria and comments on each taxa see SANDOVAL (2012).

Order Didelphimorphia: Didelphidae: Didelphinae: *Cryptonanus chacoensis* (Tate, 1931), *Cryptonanus ignitus* (Díaz, Flores, & Barquez, 2002); *Micoureus constantiae* (Thomas, 1903); *Thylamys cinderella* (Thomas, 1902), *Thylamys pallidor* (Thomas, 1902), *Thylamys pusillus* (Desmarest, 1804), *Thylamys sponsorius* (Thomas, 1902), *Thylamys venustus* (Thomas, 1902); *Monodelphis dimidiata* (Wagner, 1847), *Monodelphis kungsi* Pine, 1975.

Order Chiroptera: Noctilionidae: *Noctilio leporinus* (Linnaeus, 1758). Phyllostomidae: Phyllostominae: *Chrotopterus auritus* (Peters, 1856); *Micronycteris microtis* Miller, 1898; *Tonatia bidens* (Spix, 1823); Glossophaginae: *Anoura caudifer* (E. Geoffroy Saint-Hilaire, 1818); *Glossophaga soricina* (Pallas, 1766); Stenodermatinae: *Artibeus planirostris* (Spix, 1823); *Pygoderma bilabiatum* (Wagner, 1843); *Sturnira erythromos* (Tschudi, 1844), *Sturnira lilium* (E. Geoffroy Saint-Hilaire, 1810), *Sturnira oporaphilum* (Tschudi, 1844); Desmodontinae: *Desmodus rotundus* (É. Geoffroy Saint-Hilaire, 1810); *Diaemus youngi* (Jentink, 1893). Vespertilionidae: Vespertilioninae: *Dasypterus ega* (Gervais, 1856); *Eptesicus chiriquinus* Thomas, 1920, *Eptesicus diminutus* Osgood, 1915, *Eptesicus furinalis* (d'Orbigny & Gervais, 1847); *Histiotus laephotis* Thomas, 1916, *Histiotus macrotus* (Poeppig, 1835), *Histiotus montianus* (Philippi & Landbeck, 1861), *Histiotus velatus* (I. Geoffroy Saint-Hilaire, 1824); *Lasiurus blossevillii* (Lesson & Garnot, 1826), *Lasiurus cinereus* (Beauvois, 1796); *Myotis albescens* (E. Geoffroy Saint-Hilaire, 1806), *Myotis dinellii* Thomas, 1902, *Myotis keaysi* J. A. Allen, 1914, *Myotis nigricans* (Schinz, 1821), *Myotis riparius* Handley, 1960. Molossidae: Molossinae: *Cynomops planirostris* (Peters, 1865); *Eumops bonariensis* (Peters, 1874), *Eumops dabbenei* Thomas, 1914, *Eumops glaucinus* (Wagner, 1843), *Eumops patagonicus* Thomas, 1924, *Eumops perotis* (Schinz, 1821); *Molossops temminckii* (Burmeister, 1854); *Molossus molossus* (Pallas, 1766), *Molossus rufus* E. Geoffroy Saint-Hilaire, 1805; *Nyctinomops laticaudatus* (E. Geoffroy Saint-Hilaire, 1805), *Nyctinomops macrotis* (Gray, 1839); *Promops nasutus* (Spix, 1823); *Tadarida brasiliensis* (I. Geoffroy Saint-Hilaire, 1824).

Order Rodentia: Suborder Sciurognathi: Sciuridae: Sciurinae: *Sciurus ignitus* (Gray, 1867). Cricetidae: Sigmodontinae: Akodontini: *Akodon albiventer* Thomas, 1897, *Akodon aliquantulus* Díaz, Barquez, Braun, & Mares, 1999, *Akodon boliviensis* Meyen, 1833, *Akodon budini* (Thomas, 1918), *Akodon caenosus* Thomas, 1918, *Akodon fumeus* Thomas, 1902, *Akodon simulator* Thomas, 1916, *Akodon spegazzinii* Thomas, 1897, *Akodon sylvanus* Thomas, 1921, *Akodon toba* Thomas, 1921; *Bolomys lactens* (Thomas, 1918), *Bolomys lenguarum* (Thomas, 1898); *Oxymycterus paramensis* Thomas, 1902, *Oxymycterus wayku* Jayat, D'Elía, Pardiñas, Miotti, & Ortiz, 2008; Oryzomyini: *Holochilus chacarius* Thomas, 1906; *Oligoryzomys chacoensis* (Myers & Carleton, 1981), *Oligoryzomys destructor* (Tschudi, 1844), *Oligoryzomys flavescens* (Waterhouse, 1837); *Euryoryzomys legatus* Thomas, 1925; Phyllotini: *Andalgalomys olrogi* Williams & Mares, 1978; *Auliscomys sublimis* (Thomas, 1900); *Calomys boliviae* (Thomas, 1901), *Calomys callosus* (Rengger, 1830), *Calomys laucha* (G. Fischer, 1814), *Calomys lepidus* (Thomas, 1884), *Calomys musculus* (Thomas, 1913); *Eligmodontia bolsonensis* Mares, Braun, Corner, & Van Den Bussche, 2008, *Eligmodontia hirtipes* (Thomas, 1902), *Eligmodontia marica* Thomas, 1918, *Eligmodontia moreni* (Thomas, 1896), *Eligmodontia puerulus* (Philippi, 1896); *Graomys chacoensis* (Allen, 1901), *Graomys domorum* (Thomas, 1902), *Graomys griseoflavus* (Waterhouse, 1837); *Phyllotis alisoensis* Ferro, Martínez, & Barquez, 2010, *Phyllotis anitae* Jayat, D'Elía, Pardiñas, & Namen, 2007, *Phyllotis caprinus* Pearson, 1958, *Phyllotis osilae* J. A. Allen, 1901, *Phyllotis xanthopygus* (Waterhouse, 1837); *Salinomys delicatus* Braun & Mares, 1995; *Tapecomys primus* Anderson & Yates, 2000, *Tapecomys wolffsohni* (Thomas, 1902); Reithrodontini: *Reithrodon auritus* (G. Fischer, 1814); Thomasomyini: *Rhipidomys austrinus* Thomas, 1921; Abrothrichini: *Abrothrix andinus* (Philippi, 1858), *Abrothrix illuteus* Thomas, 1925, *Abrothrix jelskii* (Thomas, 1894); *Incertae sedis*: *Andinomys edax* Thomas, 1902; *Neotomys ebriosus* Thomas, 1894. Suborder Histicognathi: Chinchillidae: Chinchillinae: *Chinchilla brevicaudata* Waterhouse, 1848. Caviidae: Caviinae: *Cavia tschudii* Fitzinger, 1857; *Galea musteloides* Meyen, 1832; *Microcavia australis* (I. Geoffroy Saint-Hilaire & d'Orbigny, 1833), *Microcavia shiptoni* (Thomas, 1925). Octodontoidea: Ctenomyidae: *Ctenomys budini* Thomas, 1913, *Ctenomys coludo* Thomas, 1920, *Ctenomys juris* Thomas, 1920, *Ctenomys knighti* Thomas, 1919, *Ctenomys latro* Thomas, 1918, *Ctenomys occultus* Thomas, 1920, *Ctenomys opimus* Wagner, 1848, *Ctenomys saltarius* Thomas, 1912, *Ctenomys scagliai* Contreras, 1999, *Ctenomys sylvanus* Thomas, 1919, *Ctenomys tuconax* Thomas, 1925, *Ctenomys tucumanus* Thomas, 1900, *Ctenomys viperinus* Thomas, 1926. Octodontidae: *Octodontomys gliroides* (Gervais & d'Orbigny, 1844); *Octomys mimax* Thomas, 1920; *Pipanaoctomys aureus* Mares, Braun, Barquez, & Díaz, 2000. Abrocomidae: *Abrocoma budini* Thomas, 1920, *Abrocoma cinerea* Thomas, 1919.

Received 1 September 2015. Accepted 28 December 2015

ISSN 0073-4721 Article available in www.scielo.br/isz