Biogeographical analysis of rodent endemism and distributional congruence in the southern–central Andes (north-western Argentina)

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The recognition of areas of endemism (AEs) is important for conservation biology and biogeographical regionalization. Our objective was to quantitatively identify AEs and distributional congruence patterns of native rodents at the tropical/temperate transition in the central Andes. We analysed 6200 geo-referenced distributional records of 80 species in north-western Argentina using NDM/VNDM software. We found 20 AEs defined by 22 endemic species (27% of the total rodent fauna) and 34 patterns of distributional congruence in non-endemic rodents. Geographical range congruence follows two main patterns running parallel along the Andes. One is related to the humid eastern slopes of the Andes (Argentinean Yungas forest) and the other to the high Andes (Argentinean Puna plateau). Endemism was mainly restricted to the southernmost part of the Yungas forest and adjacent dryer valleys (Monte desert). Species diversity was highest in the northern sector of the Argentinean Yungas forest, where several species reach their southern distributional range. This incongruence among hotspots of diversity and endemism has also been also noted in diversity studies at continental and global scales. Our results provide a starting point for conservation planning in the southernmost Central Andes, which combines the taper of tropical diversity and range-restricted species endemic to the tropical–temperate transition. © 2014 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, **112**, 163–179.

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INTRODUCTION

Identification of areas of endemism (AEs) is important for both biogeography and conservation biology. In biogeography, the concept of endemism, which is the restricted distribution of a taxon to a particular geographical area and nowhere else, is key for biogeographical regionalization (Nelson, 1978; Lomolino, Riddle & Brown, 2006; Escalante, 2009). The congruent geographical distribution of at least two endemic taxa defines an area of endemism, which is the basic unit in evolutionary biogeographical analyses and constitutes the first step for biogeographical regionalizations (Nelson & Platnick, 1981; Humphries & Parenti, 1999; Morrone, 2009). In conservation biology, AEs are important because they contain a set of species not occurring in any other area and therefore they represent essential conservation targets, particularly if occurring in rather small geographical areas (Vane-Wright, Humphries & Williams, 1991; Linder, 1995; Peterson & Watson, 1998).

Despite the long-standing definition of AEs as the overlapping geographical distribution of endemic species (Platnick, 1991), non-spatially explicit methods have traditionally been applied to recognize them, such as parsimony analysis of endemicity (PAE) (Morrone, 1994) or cluster analysis (Linder, 2001). In this paper we adopt an approach that considers

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explicitly the spatial aspects of species distribution to identify AEs based on an optimality criterion (Szumik *et al.*, 2002; Szumik & Goloboff, 2004). Basically, this method takes into account the distributional congruence among different species by dividing the study region into grid cells and assigning endemicity values to each species according to how well their distribution matches a given set of cells (= area). The values of all species that contribute to an area are summed to obtain the endemicity value (score) of the area. The areas with higher scores are preferred. Ideally, the taxa to be used in such an analysis of endemism should be those that are maximally endemic, i.e. those whose geographical ranges are smaller than the study area. In this sense, rodents seem to be useful to analyse patterns of endemism and biographical regionalization in small geographical areas because 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). However, while tailored to identify distributional congruence of endemic species (i.e. AEs), the optimality criterion implemented in the method of Szumik *et al.* (2002) can be used to recognize prominent patterns of geographical distribution shared by several species even when non-endemic, especially when applied on small geographical areas (Aagesen *et al.*, 2009). The concordant distribution of non-endemic species may be determined either by species belonging to greater AEs or by species whose distributions are or have been affected by particular combinations of ecological or climatic factors within the geographical context of the study area. Whether the factors restricting the species ranges are a combination of present-day ecological and physical phenomena or a 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.

Traditionally, biogeographical divisions in north-western Argentina have been based on taxa (mainly plant species) characteristic to each unit (e g. Cabrera & Willink, 1973; Cabrera, 1976; Vervoorst, 1979). Quantitative evaluations of species distributional congruence are very recent compared with narrative biogeographical regionalizations that have been made for decades by different naturalists. Quantitative approaches allow the assessment of previously proposed biogeographical regionalization and even identify previously undetected AEs. Quantitative analyses of distributional congruence in northern Argentina have included selected taxa of plants, insects, reptiles, birds, and mammals, and have corroborated some conventional biogeographical divisions (Díaz Gómez, 2007; Aagesen *et al.*, 2009; Navarro *et al.*, 2009;

Sandoval, Szumik & Barquez, 2010; Szumik *et al.*, 2012). However, rodents have never been included in such quantitative analyses of endemism. Beyond the convenience of choosing rodents to analyse patterns of endemicity in small geographical areas, there are additional reasons why they are useful to analyse distributional patterns. For instance, they are present in all type of biomes from tropical moist forest to gelid highland deserts, but at the same time, they constitute quite conspicuous assemblages as a consequence of adaptation to environments (Patterson *et al.*, 1998; Mena & Vázquez-Domínguez, 2005). 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.

Here we analyse distributional records of rodent species from north-western Argentina to recognize areas of endemism and the species that characterize them. Also, we quantitatively identify patterns of geographical distribution shared by several native, but non endemic to the study area, species and relate concordant distributional patterns to traditional biogeographical divisions within the study region.

MATERIALS AND METHODS

STUDY AREA

The study area comprises an expanse of 470 184 km^2 between parallels 22 and 30°S and meridians 66 and 68°W in the southern part of the central Andes (Fig. 1). 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. Rahbek & Graves, 2001; Barthlott *et al.*, 2005; Orme *et al.*, 2005; Patterson, Solari & Velazco, 2012). The study region is located where the high diversity and endemism of the eastern Andes slopes gradually fade southward. The geographical location of north-western Argentina (NWA) in the interface between tropical and subtropical latitudes and the Andean orography on the western half of the area determine great climatic contrasts and a mosaic of different biomes, ranging from tropical rain forest to high-altitude deserts, in a rather small geographical area (Cabrera & Willink, 1973; Burkart *et al.*, 1999).

The biogeographical description outlined below follows Cabrera (1976) and Morrone (2001). The eastern lowlands are dominated by semi-arid woodlands belonging to the Chaco biogeographical province. Along the eastern slopes of the Andes occurs, as a narrow strip and on a marked elevational gradient, the montane rainforest of the Yungas biogeographical province (Fig. 1A). In the western rain shadow valleys occurs the xeric scrub of the Monte biogeographical
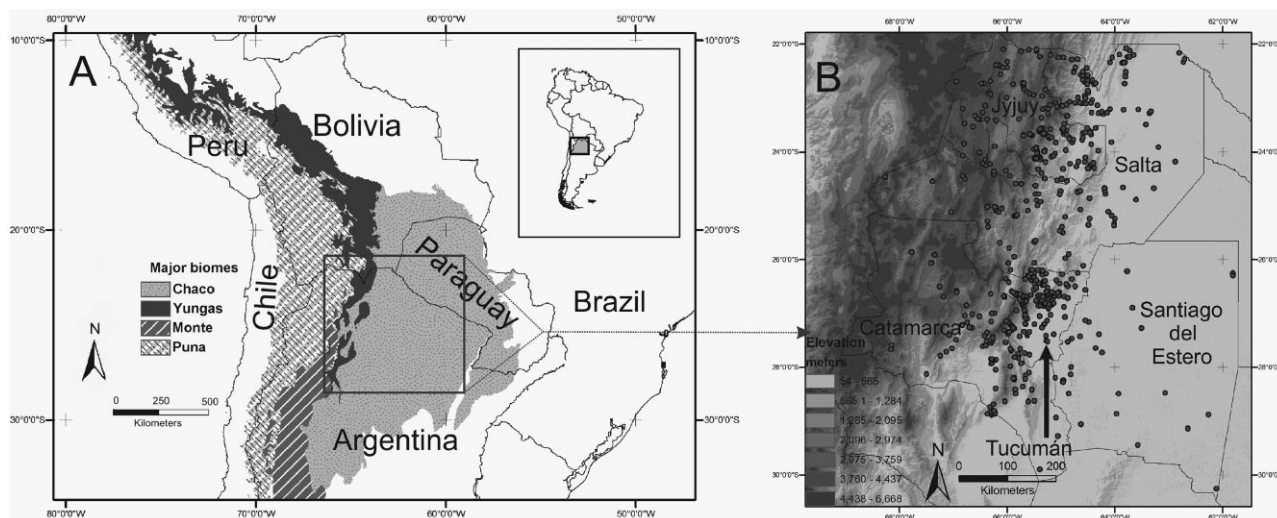
Figure 1. Study area. A, geographical location of north-western Argentina (NWA) with a simplified scheme of the principal biomes present in the study region (*sensu* Burkart *et al.*, 1999; Olson *et al.*, 2001). B, political provinces of NWA and localities of rodent occurrence.

province and on the surrounding arid mountain slopes the Prepuna biogeographical province. Finally, according to Cabrera (1976), highland desert of mountaintops can be divided into the Puna plateau, known as the Puna biogeographical province, and the biogeographical province of the High Andes in the highest and steep peaks [which Morrone (2001) considered as part of the Puna].

DATA SET

The taxonomy used herein follows that outlined in Barquez, Díaz & Ojeda (2006). All records are based on specimens and were obtained from the major Argentinean museum collections (see Supporting Information, Appendix S1). For some rodents, which are not well represented by museum specimens, we used literature records to complete our database. Literature records were included for *Abrocoma cinerea* (Thomas), *Chinchilla brevicaudata* (Waterhouse), *Coendou bicolor* (Tschudi), *C. prehensilis* (Linnaeus), *Ctenomys opimus* Wagner, *Dasyprocta punctata* (Gray), *Hydrochoerus hydrochaeris* (Linnaeus), *Lagidium viscacia* (Molina), *Lagostomus maximus* (Desmarest), *Microcavia shiptoni* (Thomas), *Myocastor coypus* (Molina), *Octodontomys gliroides* (Gervais & d'Orbigny) and *Pediolagus salinicola* (Burmeister) (Mares *et al.*, 1997; Díaz *et al.*, 2000; Díaz & Barquez, 2007; Jayat, Ortiz & Miotti, 2009; Jayat & Ortiz, 2010; Torres & Jayat, 2010; Jayat, Ortiz & González, 2013) (Appendix). Each vouchered specimen was identified to specific level by the authors. Localities were taken from museum tags or from collector catalogues. All localities were corroborated and geo-referenced using

gazetteers, maps, or satellite images and field trips. Elevational ranges of species were inferred by considering the lowest and highest elevation records for each species. To analyse distributional patterns of species outside the study area, we extrapolate the whole geographical distributional range of each species using data from taxonomic reviews and maps published by the International Union for Conservation of Nature: Red List of Threatened Species (IUCN, 2012). We divided each species distribution into three classes: endemic to the study area, reaching its southern or northern distributional edge in the study area, and widely distributed.

DISTRIBUTIONAL ANALYSIS

To identify AEs and patterns of distributional congruence of rodent species in NWA, we used the method 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 species distributions are used to identify, through an index of endemicity, among all the possible combinations of cells (= areas), those that constitute an AE. For each combination of cells, a score between 0 and 1 is calculated for all species. The species score depends on the fit of the individual species to the given combination of cells (see Szumik *et al.*, 2002; Szumik & Goloboff, 2004). The endemicity score of a given area (combination of cells) is the sum of the individual species scores. Only the areas with highest scores are retained. This optimality criterion is implemented in

the computer program NDM and its viewer VNDM (Goloboff, 2005; available at http://www.zmuc.dk/public/phylogeny).

The optimality criterion implemented in NDM was tailored to identify AEs based on its classic definition as places where two or more taxa are found together and nowhere else (Platnick, 1991). However, the method can also be applied to discover patterns of distributional congruence of species whose ranges exceed the study region size (Aagesen *et al.*, 2009). The spatial congruence of several species restricted to some parts of the study area suggests the occurrence of causal factors affecting their distributions. The distributional congruence of species not endemic to the study area may be representing parts of larger AEs, local co-occurrence by particular combinations of ecological or climatic factors, or an artefact due to unevenness of sampling localities. It is beyond the scope of this study to identify the causal factors of the distributional concordances identified. Thus, we will consider two area categories, as follows: AEs (defined only or mostly by sympatric endemic species) and local patterns of distributional congruence (LPDCs, defined only or mostly by sympatric species not endemic to the study area).

We analysed our matrix of geo-referenced data using grid cells of four different sizes, 1°, 0.75°, 0.5° and 0.25° per side, and rectangular cells of 0.75 × 0.25° latitude–longitude. The use of several grid sizes and shapes increases the chance of finding different areas given the topographical complexity of the study area; 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). Additionally, grid sizes and shapes used in this analysis were already used for the study area, facilitating comparisons with previous studies (e.g. Díaz Gómez, 2007; Aagesen *et al.*, 2009; Navarro *et al.*, 2009; Sandoval *et al.*, 2010; Szumik *et al.*, 2012). In preliminary analyses of our data set, we found that by increasing cell size, species that are not actually sympatric may be included in a given area. Incorporation of many species as endemic to an area just based on their marginal records was a frequent imprecision when using coarse grid cells. These species generally presented low individual values of endemicity, and could obscure the true pattern of species composition represented by that set of cells. Therefore, for the coarser grid cells (square cells of 1° and 0.75° per side) we set minimum species scores as 0.5. That is, only those species that contribute to an area with an individual value of endemicity equal to or greater than 0.5 finally contribute to that area. For the finer grid cells we did not set any minimum

species scores. Contrary to coarse cells, if cells are too small the number of artificially empty cells increases and reduces 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 (Szumik & Goloboff, 2004; Casagranda *et al.*, 2009; Arias, Szumik & Goloboff, 2011). Therefore, we analysed our matrix considering different filling values for assumed and inferred presences for smaller cells (square cells of 0.5° and 0.25° per side). An assumed presence implies that, even if a species has not been recorded in a cell, its presence is assumed due to its proximity to records in neighbouring cells; an inferred presence is implemented by the method itself when a species is absent from one cell but present in surrounding cells (Szumik & Goloboff, 2004). For a brief explanation on how the algorithm works see Aagesen *et al.* (2009).

Grid origin was arbitrarily defined and located at 70°W and 20°S. We carried out the distributional analysis through an heuristic (not exhaustive) search using the default NDM parameters: searching for groups of cells by adding/eliminating one cell at a time and saving groups defined by two or more endemic species with scores higher or equal to 2.0. When candidate areas shared more than 50% of their defining species, only the area with the highest score was retained. We obtained consensus areas by combining candidate areas that shared at least 50% of their defining species using the loose consensus rule in VNDM (see Aagesen, Szumik & Goloboff, 2013).

The concordant distribution patterns were evaluated in the context of traditional biogeographical 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.

RESULTS

The analysis of 6116 geo-referenced records of 80 rodent species (35 genera and 11 families) from NWA resulted in 65 consensus areas. Two large areas almost equivalent to the study were not considered in the following characterization. The remaining 63 areas represent either AEs in the strict sense or LPDCs characterized by 61 species of 30 genera.

Twenty-two species (27.5% of all study area rodent fauna) are endemic to the study area, of which 19 species defined AEs (Appendix). Twenty consensus areas are defined mostly by endemic species, thus constituting AEs in the strict scene. All of these areas are located in the southern part of the study area,
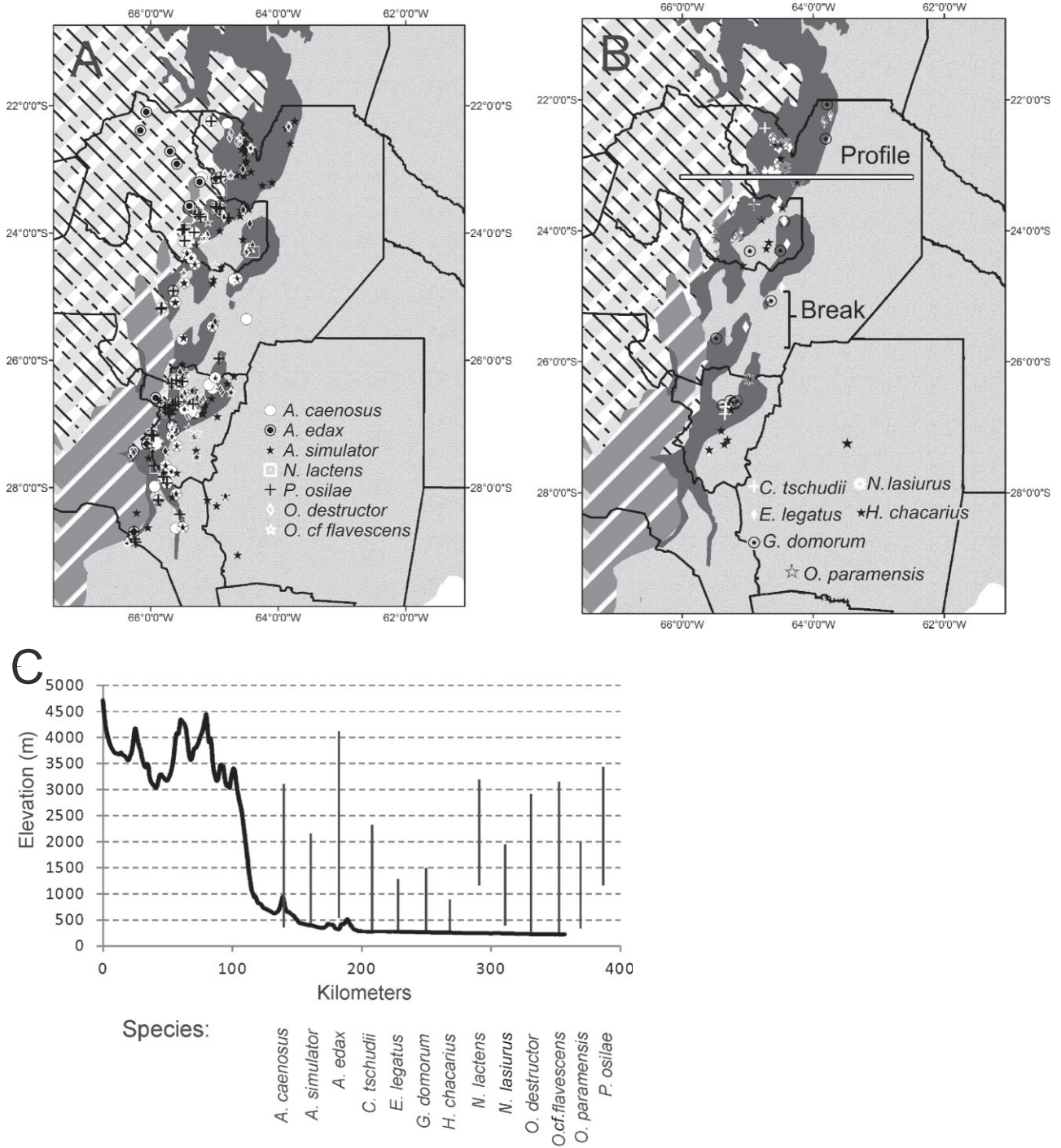
either on the eastern moist Andean slopes and lowlands or on the western dry valleys. Thirty-four consensus areas are determined by species whose distributions exceed the study area, and thus we consider them as LPDCs. These areas fall into two main patterns running parallel to the Andes (i.e. orientated north–south), one on the eastern Andean slopes and the other on the western highlands; both have smaller areas nested within them. The remaining nine consensus areas are grouped into two patterns, one in the northern and the other in the southern part of the study area. These patterns, running transverse to the Andes (i.e. east–west), lump the previously identified consensus areas on eastern moist Andean slopes and the western dry valley and highlands. The defining species are also combinations of the lowland and highland species groups previously identified, and thus we consider these to be spurious areas (SAs).

LOCAL PATTERNS OF DISTRIBUTIONAL CONGRUENCE

Widespread Eastern Andean Slopes ('Argentinean Yungas')

Ten consensus areas were equivalent to this pattern, comparable to the Argentinean Yungas biogeographical province (Table 1; Fig. 2). Of these ten LPDCs, five were continuous areas (Fig. 2A) and five were disjunct areas. The disjunction in all cases was located in the same geographical region, at the Central sector of the Argentinean Yungas (Fig. 2B). The continuous areas were obtained with only one grid size and different filling values, while disjunct areas were obtained with three grid sizes and different filling values (Table 1).

Thirteen species characterize these LPDCs. Six species characterize both continuous and disjunct areas [*Akodon caenosus* Thomas, *A. simulator* Thomas, *Necromys lactens* (Thomas), *Oligoryzomys destructor* (Tschudi), *O.* cf. *O. flavescens* (Waterhouse), and *Phyllotis osilae* (JA Allen)], one species characterizes only continuous areas (*Andinomys edax* Thomas) and six species characterize only disjunct areas [*Cavia tschudii* Fitzinger, *Euryoryzomys legatus* Thomas, *Graomys domorum* (Thomas), *Holochilus chacarius* Thomas, *Necromys lasiurus* (Lund), and *Oxymycterus paramensis* Thomas]. There are no endemic species characterizing these areas, 11 species reach their southern distributional edge in the study area, and two are widely distributed (Table 2).

Widespread Western High Andes ('Puna')

Six consensus areas equivalent to this pattern, comparable to the Argentinean Puna biogeographical province (Fig. 3), were obtained with two grid sizes (Table 1).

Table 1. Summary of the consensus areas corresponding to the six general patterns and the two groups of spurious areas, indicating grid size and search parameters

Cell size	1° × 1°	0.75° × 0.75°	0.5° × 0.5°					0.25° × 0.25°					0.75° × 0.25°		Total
Area/Filling value (A I)	00 00	00 00	00 00	10 30	30 50	50 70	70 90	00 00	10 30	30 50	50 70	70 90	00 00	70 90	
1 Yungas	1D	1D	2D	1C	1C	1C	1D, 2C	–	–	–	–	–	–	–	10
2 Northern Yungas	1	2	4	2	1	1	3	–	–	–	–	–	2	1	17
3 Southern Yungas	–	1	2	1	1	1	1	2	2	1	1	1	2	2	18
4 Monte	1	–	–	–	–	1	–	–	–	–	–	–	–	–	2
5 Puna	4	2	–	–	–	–	–	–	–	–	–	–	–	–	6
6 High Andes	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1
Spurious Area 1	1	–	–	1	–	1	1	–	–	1	–	–	–	1	6
Spurious Area 2	2	–	–	–	–	–	–	–	–	–	–	1	–	–	3
Total	10	6	8	5	3	5	9	2	2	2	1	2	4	4	63

Filling values are coded as: A, assumed presences; I, inferred presences. For the areas corresponding to the Argentinean Yungas, continuous and disjunct areas are indicated as C for continuous and D for disjunctive areas.

Figure 2. Widespread Eastern Andean Slopes ('Argentinean Yungas'). A, occurrence localities of the defining species of a distributional pattern comparable to the entire Yungas of Argentina as a continuous area. B, occurrence localities of the defining species of a distributional pattern comparable to the entire Yungas of Argentina as a disjunctive area (note that all species, except *A. edax*, defining the continuous pattern also support the disjunct pattern). C, elevational range of all Argentinean Yungas-defining species.

Table 2. Summary of the consensus areas corresponding to the Argentinean Yungas indicating defining species, number of individual areas where each species is present, individual endemicity values (as ranges), and elevational range and distributional limit of each species

Species	No. of areas (of 10)	Individual score	Distributional range	Altitudinal range (m)
A. caenosus	6	0.000–0.882	SL	400–3100
A. simulator	3	0.000–0.764	SL	400–3000
A. edax	1	0.000–0.685	SL	1000–4500
C. tschudii	4	0.526–0.766	SL	371–2652
E. legatus	1	0.000–0.795	SL	407–1270
G. domorum	3	0.000–0.746	SL	1000–1200
H. chacarius	2	0.000–0.687	WD	300–700
N. lactens	4	0.000–0.806	SL	1400–3200
N. lasiurus	4	0.636–1.000	SL	1700–1900
O. destructor	5	0.551–0.814	SL	400–2800
O. cf flavescens	6	0.000–0.862	WD	400–2800
O. paramensis	4	0.417–0.825	SL	1400–3000
P. osilae	5	0.000–0.907	SL	1400–3200

SL, the southern limit of the species distributional range is located in the study area; WD, the species has wider distributional range than the others in the study area and surrounding areas.
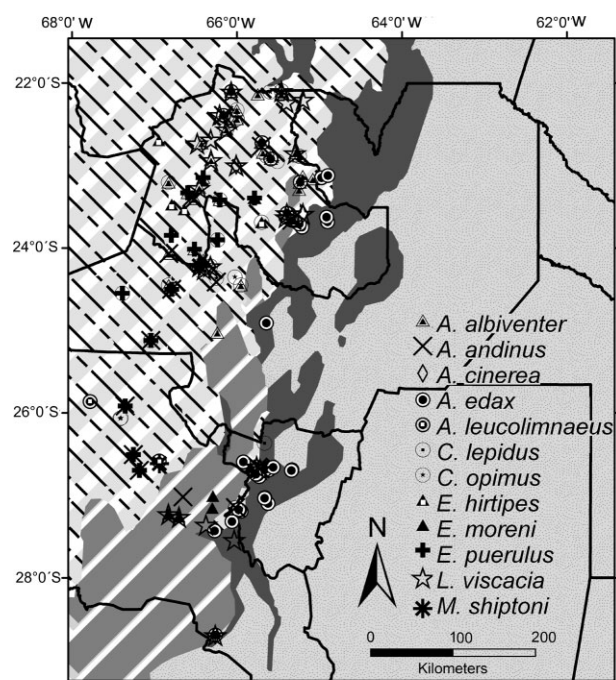
Figure 3. Widespread Western High Andes ('Puna'). Occurrence localities of the defining species of the distributional pattern comparable to the Puna of north-western Argentina.

Twelve species characterize these LPDCs. There are two endemic species, five species reach their southern distributional edge in the study area, and five are widely distributed (Table 3).

North-eastern Andean Slopes ('Northern Argentinean Yungas')
Seventeen consensus areas were equivalent to this pattern, comparable to the Northern sector of the Argentinean Yungas biogeographical province (Table 1; Fig. 4). These LPDCs were recovered with all grid sizes and different filling values (Table 1).

Nineteen species characterize these LPDCs. This is the largest set of defining species for the study area. There are two endemic species, 14 species reach their southern distributional edge in the study area, and three are widely distributed (Table 4).

North-western High Andes ('High Andes')
One consensus area was equivalent to a small patch in the High Andes of the north of the study area (Table 1; Fig. 5). This LPDC was recovered with only one grid size and only one filling value (Table 1).

Five species characterize this LPDC, one of them being endemic to the study area, three reaching their southern distributional edge in the study area, and one being widely distributed (Table 5). All these species have few records in NWA, all around the study area.

AREAS OF ENDEMISM

South-eastern Andean Slopes ('Southern Argentinean Yungas')
Eighteen consensus areas were equivalent to this pattern, comparable to the Southern sector of the Argentinean Yungas biogeographical province

Table 3. Summary of the consensus areas corresponding to the Puna indicating defining species, number of individual areas where each species is present, individual endemicity value (as ranges), and the elevational range and distributional limit of each species

Species	No. of areas (of 10)	Individual score	Distributional range	Altitudinal range (m)
A. cinerea	2	0.000–0.786	WD	3800–5000
A. andina	2	0.000–0.844	WD	3500–4300
A. albiventer	1	0.818	SL	2400–5000
A. leucolimnaeus	1	0.750	E	3100–3500
A. edax	2	0.000–0.711	SL	1000–4500
C. lepidus	2	0.000–0.750	SL	2600–5000
C. opimus	3	0.000–0.909	WD	2500–5000
E. hirtipes	4	0.536–0.833	SL	2408–4343
E. moreni	3	0.000–0.682	WD	1200–2300
E. puerulus	3	0.000–0.833	SL	3450–4343
L. viscacia	3	0.000–0.900	WD	2500–5100
M. shiptoni	3	0.000–0.750	E	3000–4000

SL, the southern limit of the species distributional range is located in the study area; E, the species is endemic to the study area; WD, the species has wider distributional range than the others in the study area and surrounding areas.

(Table 1; Fig. 6). These areas were recovered with two grid sizes and different filling values (Table 1).

There are 14 supporting species. Twelve are endemic species and two species reach their northern distributional edge (Table 6).

South-western High Andes ('Monte Desert')
Two consensus areas were equivalent to a patch of the Monte biogeographical province in the south of the study area (Table 1; Fig. 7). These AEs were recovered with two grid sizes and one combination of filling values (Table 1).

One of these areas is characterized by four species: *Andalgalomys olrogi* Williams & Mares, *Ctenomys knighti* Thomas, *Pipanacoctomys aureus* Mares, Braun, Barquez & Díaz, and *Salinomys delicatus* Braun & Mares. The other area is characterized by three species: *Ctenomys scagliai* Contreras, *Eligmodontia bolsonensis* Mares, Braun, Corner & Van Den Bussche, and *Akodon leucolimnaeus* Cabrera. There are five endemic species characterizing these AEs; meanwhile, two species reach their northern distributional edge in the study area (Table 7).

SPURIOUS AREAS

North-eastern Andean Slopes merged with Northern-western High Andes ('SA 1').
Six areas equivalent to this pattern were obtained, with three different cell sizes, in the north of the study area (Fig. 8A). These areas were characterized by 15 species, which can be divided in two sets: a highland group of species [*Abrothrix jelskii* (Thomas), *Akodon albiventer* Thomas, *A. boliviensis* Meyen,

Auliscomys sublimis (Thomas), *Ctenomys budini* Thomas, *Neotomys ebriosus* Thomas, *Octodontomys gliroides*, and *Phyllotis caprinus* Pearson] and a lowland or sylvan set [*A. budini* (Thomas), *A. fumeus* Thomas, *A. sylvanus* Thomas, *Coendou bicolor*, *Sciurus ignitus* (Gray), *Tapecomys primus* Anderson & Yates, and *T. wolffsohni* (Thomas)] (Fig. 8B).

South-eastern Andean Slopes merged with South-western High Andes ('SA 2')
Three areas considered as spurious were obtained in the south of the study area (Fig. 8C). These areas are characterized by 13 species: *Abrothrix illutea* Thomas, *Andalgalomys olrogi*, *Ctenomys coludo* Thomas, *C. knighti*, *C. saltarius* Thomas, *C. scagliai*, *C. tuconax* Thomas, *C. tucumanus* Thomas, *Eligmodontia bolsonensis*, *Oxymycterus wayku* Jayat, D'Elía, Pardiñas, Miotti & Ortiz, *Phyllotis alisosiensis* Ferro, Martínez & Barquez, *Pipanacoctomys aureus*, and *Salinomys delicatus*. Eight species correspond to the western arid slopes and five to the moist eastern slopes (Fig. 8D).

DISCUSSION

EASTERN ANDEAN SLOPES PATTERN

The widespread Eastern Andean Slopes pattern allows us to identify the entire latitudinal extension of the Yungas forest as a discrete biogeographical unit in the NWA geographical context. This is a stable pattern given that it was recovered with different cell sizes and shapes (Table 1). However, none of the 13 species that characterize the Yungas forest, either as a continuous
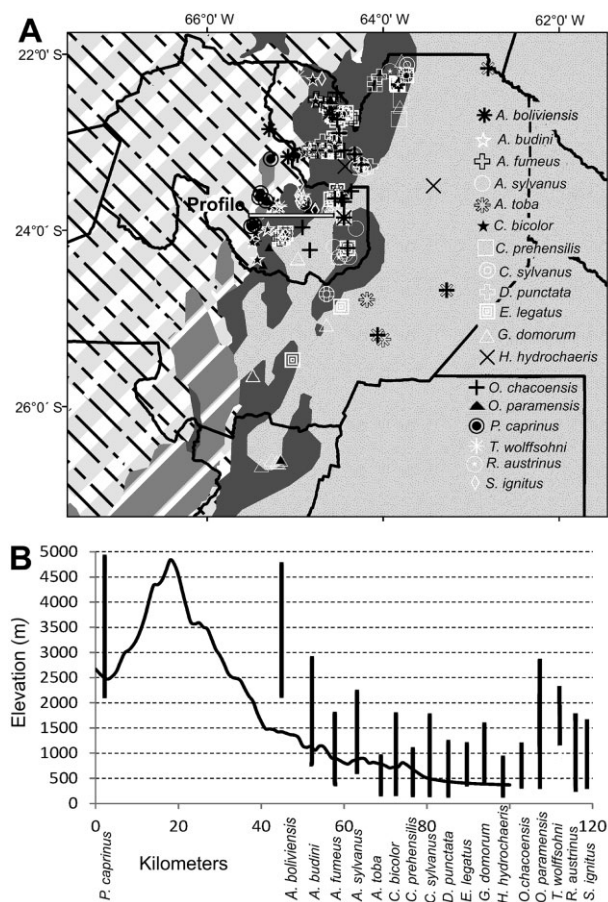
Figure 4. North-eastern Andean Slopes ('Northern Argentinean Yungas'). A, occurrence localities of the defining species of the distributional pattern comparable to the Northern sector of the Argentinean Yungas. B, elevational range of the defining species.

or as a disjunct area, is exclusive of the NWA Yungas. Moreover, some are not exclusive to the rainforest; for instance, *Holochilus chacarius* and *Oligoryzomys* cf. *O. flavescens* are widely distributed lowland species (Table 2), and their presence as LPDC-defining species may be due to sampling artefacts. The remaining 11 defining species reach their southernmost distributional range in NWA Yungas (Table 2). Thus, the Yungas of NWA (Fig. 2) may be part of a larger AE extending beyond the limits of our study area. This may well indicate that the Yungas forest in NWA is the tail of a broader area that extends towards the north through the Bolivian Yungas and probably to southern Peru. The northern continuity of NWA Yungas as an AE should be assessed by integrating Bolivian and Peruvian rodent faunas within a quantitative analysis. Alternatively, the recognition of distributional congruence in the southern limit of the species distributions may be due to a similar response to a unique

combination of ecological and historical factors restricting species ranges that do not necessarily affect in the same way these species northwards. This has important implications for biodiversity conservation. The southernmost extension of the Yungas forest has an inherent environmental gradient associated with its passage from tropical latitudes (22°S on the Bolivian border) to subtropical latitudes (29°S on its southern limit) and progressively interdigitates into a matrix of temperate arid/semi-arid landscapes. The conservation of populations inhabiting transitional habitats could maximize the species probability of viable responses to changing environmental conditions, such as those expected to be driven by climate change (Smith *et al.*, 2001). In this sense, we identified a set of species with geographical range concordance of their southern populations. Additionally, the Yungas forest has an essential characteristic, which is the strong elevational gradient ranging from 500 m up to 3500 m and passing from dense rainforest through temperate forest to grasslands. The elevational range of the defining species (Fig. 2C) reinforces the importance of this area as a complement to biodiversity hotspots for regional conservation.

The recognition of the disjunct pattern was also reported for bats and marsupials in NWA Yungas (Sandoval *et al.*, 2010). The rainforest in NWA is not continuously distributed, but patchy and in close association with mountain ranges (Fig. 1). Thus, disjunct populations of sylvan species might be a reasonable outcome. Additionally, the location of the disjunction is always situated in the central Yungas (Fig. 2B) where the forest becomes narrower because of the lower elevation of the mountain ranges and the presence of broad intermountain dry valleys. However, note that there is a low density of sampled localities in this region (Fig. 1). This could lead to gaps in our knowledge of species distributions in the Central sector of the Argentinean Yungas. In fact, almost half of the species that characterize the Argentinean Yungas along its entire latitudinal extension (six species) characterize both continuous and disjunct areas. Thus, at this point the disjunction of the Argentinean Yungas might be seen as a sampling artefact rather than isolated populations inhabiting the Northern and the Southern forest sectors but not the Central one. Further exploration of this region (e.g. Sierras de Metan, de Rosario de la Frontera and Candelaria) should clarify whether the disjunction is real, or if the central Yungas of NWA is part of the northern or southern Yungas, if it is a transition between these two areas or even a third AE nested within the entire Yungas forest.

The northernmost sector of the Yungas of NWA (North-eastern Andean Slopes; Fig. 4), near the Bolivian border, is just traversed by the Tropic of Capricorn.

Table 4. Summary of the consensus areas corresponding to the Northern Argentinean Yungas indicating defining species, number of individual areas where each species is present, individual endemicity values (as ranges), and the elevational range and distributional limit of each species

Species	No. of areas (of 17)	Individual score	Distributional range	Altitudinal range (m)
A. boliviensis	9	0.000–0.906	SL	2400–4200
A. budini	10	0.000–0.979	SL	1500–2600
A. fumeus	10	0.000–1.000	SL	670–3500
A. sylvanus	3	0.000–0.800	E	700–2400
A. toba	4	0.000–0.727	WD	255–935
C. bicolor	5	0.000–0.825	SL	350–1700
C. prehensilis	1	0.000–0.750	SL	355–1100
C. sylvanus	11	0.000–1.000	E	304–1720
D. punctata	10	0.000–0.907	SL	300–1500
E. legatus	7	0.000–1.000	SL	407–1270
G. domorum	2	0.000–0.766	SL	1000–1200
H. hydrochaeris	4	0.000–0.716	WD	255–900
O. chacoensis	4	0.000–0.909	WD	255–1270
O. paramensis	1	0.000–0.714	SL	700–3000
P. caprinus	5	0.000–0.790	SL	2100–4500
R. austrinus	8	0.000–0.900	SL	300–2600
S. ignitus	9	0.000–1.000	SL	472–1590
T. primus	6	0.000–0.875	SL	1000–1500
T. wolffsohni	8	0.000–0.844	SL	1180–23360

SL, the southern limit of the species distributional range is located in the study area; E, the species is endemic to the study area; WD, the species has wider distributional range than the others in the study area and surrounding areas.
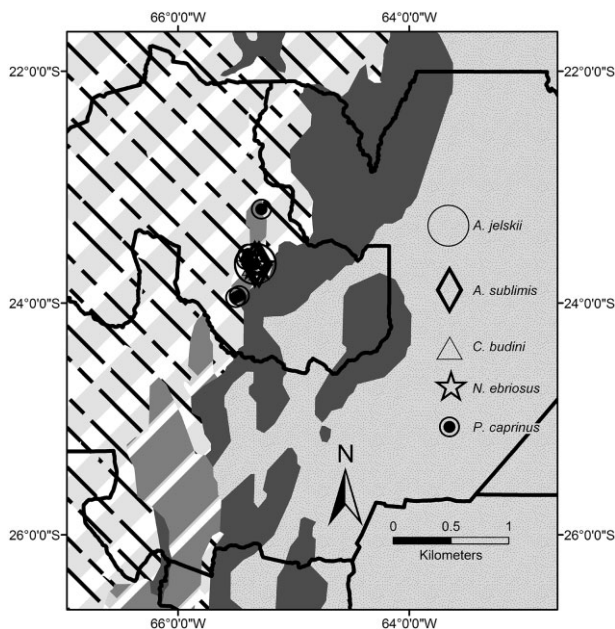

Figure 5. North-western High Andes ('High Andes'). Occurrence points of the defining species of the distributional pattern comparable to the High Andes of north-western Argentina.

Certainly, the northern part is the richest sector of the NWA Yungas forest, gradually becoming impoverished southward (Ojeda & Mares, 1989; Ojeda *et al.*, 2008). However, while species-rich, this area has few species endemic to NWA. Only two of the 19 defining species are restricted to NWA (*Akodon sylvanus* and *Ctenomys sylvanus* Thomas) and 14 reach their southern distributional limit in this area. Thus, the Tropic of Capricorn marks an evident distributional limit for several rodent species. The other three species (*A. toba* Thomas, *Hydrochoerus hydrochaeris*, and *Oligoryzomys chacoensis* Myers & Carleton) are widely distributed lowland species (Table 3). Note that the records of these species are the most eastern ones of the area and furthermore are restricted to low elevations (Fig. 3). These species may therefore be shown to extend their ranges further east and south, if more locations are sampled in the Dry Chaco (Table 3, Fig. 3). For bats and marsupials, the Northern sector of the Argentinean Yungas is also recovered as a nested area within the entire latitudinal extension of NWA (Sandoval *et al.*, 2010).

By contrast, the South-eastern Andean Slope pattern (Fig. 6) is impoverished in terms of defining species but very rich in endemics. Of the 14 species that define the southern counterpart of this pattern, 12 are endemic to the study area (Table 6). In fact,

Table 5. Summary of the consensus areas corresponding to the High Andes, indicating defining species, number of individual areas where each species is present, individual endemicity value (as ranges), and the elevational range and distributional limit of each species

Species	No. of areas (of 1)	Individual score	Distributional range	Altitudinal range (m)
A. jelskii	1	0.950	SL	4009–4370
A. sublimis	1	0.950	SL	3800–4296
C. budini	1	0.950	E	4209
N. ebriosus	1	0.950	WD	3900–4209
P. caprinus	1	0.528	SL	2100–4500

SL, the southern limit of the species distributional range is located in the study area; E, the species is endemic to the study area; WD, the species has wider distributional range than the others in the study area and surrounding areas.
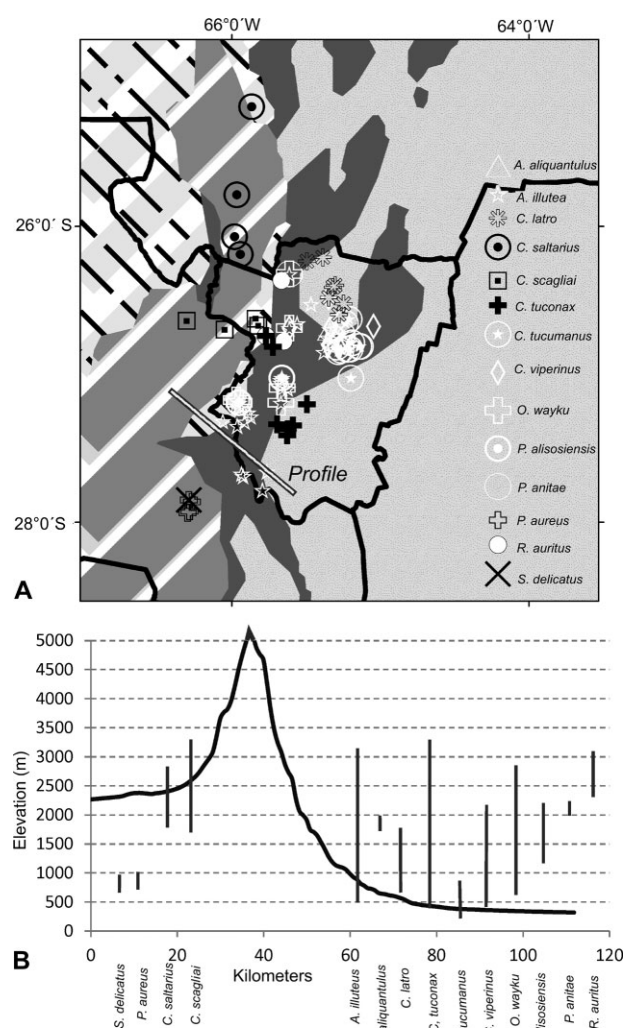
Figure 6. South-eastern Andean Slopes ('Southern Argentinean Yungas'). A, occurrence localities of the defining species of the distributional pattern comparable to the Southern sector of the Argentinean Yungas. B, elevational range of the defining species.

only nine species inhabit the eastern sylvan slopes corresponding to the southern Yungas forest (see Ferro, 2013, for a detailed compilation of rodents inhabiting the eastern Andean slopes). However, we considered this as a valid AE based on their high endemicity score and repeated occurrence (Table 4). The geographical proximity of the desert on the western slopes of the Aconquija and Cumbres Calchaquíes mountain ranges allowed *Ctenomys saltarius*, *C. scagliai*, *Pipanacoctomys aureus*, and *Salinomys delicatus* to contribute to the score for this area, even though they are not distributed on the moist eastern slopes (Fig. 4B). Notoriously, with the exception of *C. scagliai*, all these were found only in one of the 18 consensus areas and with low individual endemicity values (see Table 4). The Southern sector of the Yungas forest of NWA has been differentiated by phytogeographers as an impoverished version of the Northern sector rather than based on exclusive floral elements (Cabrera, 1976; Morales, 1996; Brown *et al.*, 2001). Our analysis revealed the Southern sector of the Argentinean Yungas as a distinctive AE, characterized by nine endemic species of rodents (Fig. 4B). Additionally, this area was recovered for insects (Navarro *et al.*, 2009), and for a taxonomically diverse data set when analysed using quantitative approaches (Szumik *et al.*, 2012). The occurrence of range-restricted species together with the southern-most populations of species distributed in the entire Yungas forest makes this area a significant target for biodiversity conservation.

Dry Chaco: why not a regional pattern of distributional congruence?

In our analysis based in rodent distribution we fail to recognize the Chaco biogeographical province either as an AE or as an LPDC. Although some rodent distributions may be coincident with the Chaco province [e.g. *Akodon toba*, *Graomys chacoensis* (JA Allen), *Holochilus chacarius*, and *Oligoryzomys chacoensis*],

Table 6. Summary of the consensus areas corresponding to the Southern Argentinean Yungas, indicating defining species, number of individual areas where each species is present, individual endemicity value (as ranges), and the elevational range and distributional limit of each species

Species	No. of areas (of 18)	Individual score	Distributional range	Altitudinal range (m)
A. illutea	6	0.000–0.938	E	540–2800
A. aliquantulus	5	0.271–0.875	E	1700–1900
C. latro	12	0.000–0.833	E	600–1100
C. saltarius	1	0.600	E	1600
C. scagliai	7	0.000–0.700	E	1886–2739
C. tuconax	12	0.000–0.900	E	361–3100
C. tucumanus	12	0.000–0.875	E	400–600
C. viperinus	17	0.000–1.000	E	700–2300
O. wayku	11	0.000–0.800	E	800–2800
P. alisosiensis	6	0.000–0.944	E	1200–2200
P. anitae	2	0.000–0.731	E	2300–2400
P. aureus	1	0.000–0.271	E	735
R. auritus	12	0.000–0.972	NL	2400–3100
S. delicatus	1	0.000–0.271	NL	300–500

E, the species is endemic to the study area; NL, the northern limit of the species distributional range is located in the study area.
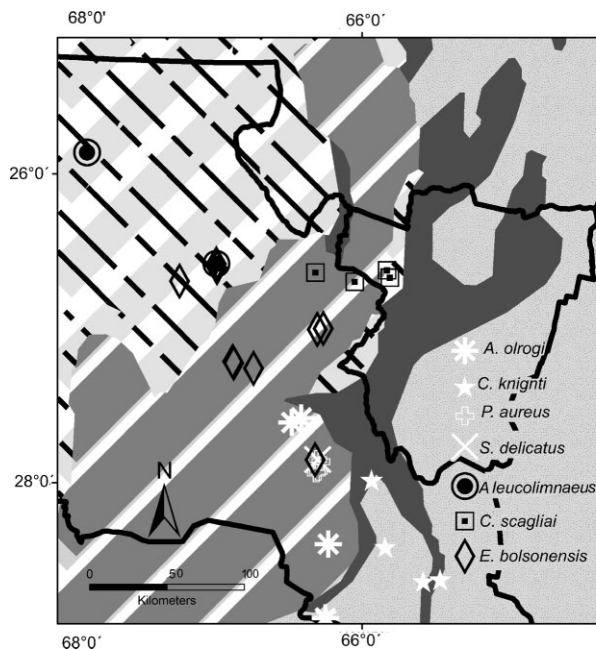
Figure 7. South-western High Andes ('Monte desert'). Occurrence localities of the defining species of the distributional pattern corresponding to the Monte of north-western Argentina.

the sampling localities are too scattered and prevent the identification of a sympatric distribution pattern (Fig. 1), apparently even for the largest grids and higher filling options.

WESTERN HIGH ANDES PATTERNS

The Puna province is a vast tableland extending along the entire western half of NWA and to the north into Bolivia. In this study, we recognize the Puna as a discrete biogeographical unit in the geographical context of NWA (the Widespread Western High Andes pattern; Fig. 6). However, only two of the 12 defining species are endemic to the study area: *Akodon leucolimnaeus* and *Microcavia shiptoni*. Thus, the Puna of NWA is part of a larger AE that is probably coincident with the physiographical Puna. Half of the defining species reach their southern limit in NWA. However, large areas of these highlands remain unexplored and thus the distributional limits of the species remain loosely known (Ortiz *et al*., 2000; Jayat *et al*., 2011). Further exploration of the Puna and the surrounding mountaintops should clarify the existence of different AEs associated with mountain-tops on the highlands of NWA.

The Monte biogeographical province in NWA occurs on the arid western (rain shadow) slopes. As the Yungas forest reaches its southern tip on the humid eastern Andean slopes in NWA, the Monte province reaches its northernmost extension on the west-facing slopes of the same mountain ranges (Fig. 1). The two consensus areas coincident with the Monte province detected in this analysis (the South-western High Andes pattern; Fig. 7) are defined by species either endemic to the study area (*Akodon leucolimnaeus*, *Ctenomys knighti*, *C. scagliai*, *Eligmodontia bolsonensis*, and *Pipanacoctomys aureus*) or reaching

Table 7. Summary of the consensus areas corresponding to the Monte desert, indicating defining species, number of individual areas where each species is present, individual endemicity value (as ranges), and the elevational range and distributional limit of each species

Species	No. of areas (of 2)	Individual score	Distributional range	Altitudinal range (m)
A. leucolimnaeus	1	0.750	E	3100–3500
A. olrogi	1	0.653	NL	396–1172
C. knighti	1	0.376	E	2000
C. scagliai	1	0.750	E	1886–2739
E. bolsonensis	1	0.625	E	2186–2249
P. aureus	1	0.776	E	735
S. delicates	1	0.776	NL	735

E, the species is endemic to the study area; NL, the northern limit of the species distributional range is located in the study area.

their northernmost limit of distribution in NWA (*Andalgalomys olrogi* and *Salinomys delicatus*). Thus, as well as the southern Yungas forest, the Monte of NWA combines the occurrence of range-restricted and the northernmost populations of species distributed southwards in the entire biogeographical province.

Spurious areas

Two sets of areas were defined by species that support previously detected areas and we considered them as spurious. These areas combine consensus areas corresponding to well-defined main patterns. Spurious area 1 combines the Northern Argentinean Yungas and High Andes (Fig. 8A), and spurious area 2 the Southern Argentinean Yungas and Monte Desert (Fig. 8C). These spurious areas are a probable outcome of using the 'loose' consensus rule (Aagesen *et al.*, 2013). 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. The tight rule may be more realistic in small-scale studies while the loose consensus may be applied in large-scale studies (Aagesen *et al.*, 2013). Thus, the 'loose' consensus rule is a useful tool for detecting gradual overlapping distribution patterns and replacement among areas. Therefore, these spurious areas may well be indicating a transition zone between the two main patterns. For instance, in the northern part of the study region, spurious area 1, some species such as *Akodon boliviensis* and *Phyllotis caprinus* inhabit a narrow zone between the two main areas. Spurious area 1 includes a strong elevational gradient in a very short geographical distance and most of the defining species show marked altitudinal segregation (see Fig. 8B). In the southern part of the study region the two areas defined by endemic species to the Southern Argentinean Yungas and the Monte Desert

are merged into spurious area 2. This area is defined by a set of species that have similar elevational ranges, but inhabit either the forested eastern slopes (Yungas) or the deserted western slopes and valleys (Monte). These are totally different biomes and the two sets of species which define this pattern are allopatric in nature (Fig. 8C, D). Thus, knowledge of the biology of each species seems to be very important when generalizing distributional data in small geographical areas, particularly when strong environmental gradients are present.

Some taxonomic considerations

Taxonomic knowledge is fundamental to discovering realistic biodiversity patterns and to arriving at firm conclusions. The taxonomic status of NWA rodent populations has been matter of continuous revision and debate over the last decade.

Although several advances have been made on rodent taxonomy and distribution, there remain some taxonomic uncertainties that should be solved by type specimen comparisons. We therefore decided to work only with specimens reviewed by ourselves. This choice may lead to the omission of some records, particularly those from recently added and poorly known species, but much more is gained in accuracy and repeatability of our data analyses. Further advances on taxonomic and distributional knowledge will surely refine the main patterns reported here.

CONCLUSIONS

Our analyses showed two main patterns of rodent endemism. Both run parallel along the Andes throughout the study region. One is related to the eastern slopes of the Andes (Yungas forest) and the other to high Andes and adjacent dry valleys (Puna
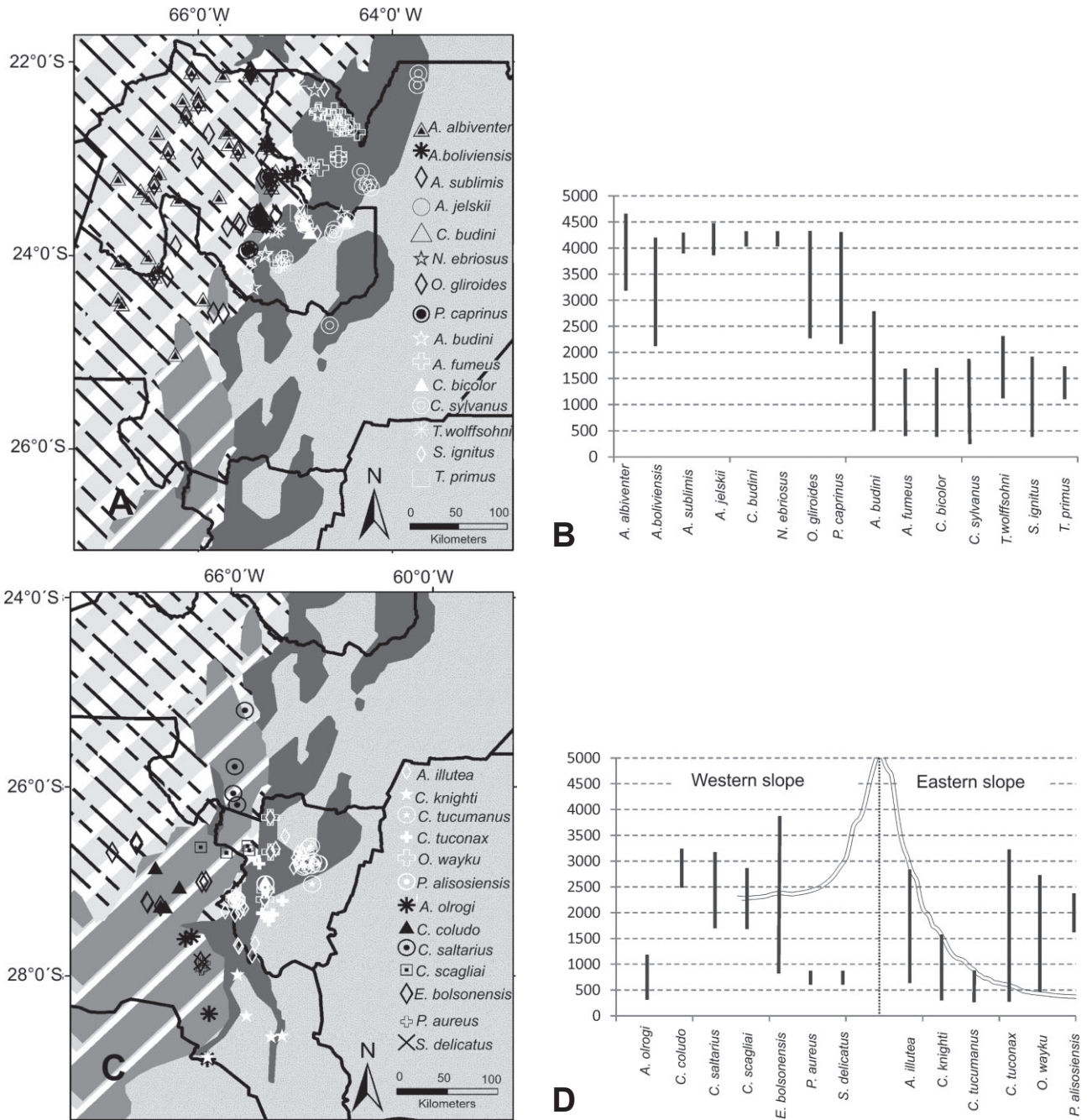
Figure 8. Spurious areas. A, occurrence localities of the defining species of 'spurious area 1'. B, elevational range of the defining species of 'spurious area 1'. C, occurrence localities of the defining species of 'spurious area 2'. D, elevational range of the defining species of 'spurious area 2'.

Plateau and Monte Desert). This is concordant with the two biogeographical regions present in the study area: the Neotropical and the Andean (Morrone, 2001). Furthermore, these two main patterns are subdivided into nested areas. Species diversity is highest within the Yungas forest in the northern part

of the study region where several species reach their southern distribution limit. Endemism is, by contrast, mainly restricted to the isolated southernmost part of the Yungas forest and adjacent dryer valleys. This pattern of incongruence among hotspots of diversity and endemism, reported here for a rather local-scale

study, has also been noted in global and continental diversity studies (e.g. Orme *et al*., 2005; Swenson *et al*., 2012) and this incongruence presents a major challenge for conservation as protected area systems often focus on hotspots of species diversity (Whittaker *et al*., 2005). Our results provide a starting point for conservation planning in this area, which combines the taper of tropical diversity and range-restricted species endemic to the tropical–temperate transition.

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APPENDIX

Rodent species included in the analysis. The taxonomy used herein mainly follows Barquez *et al*. (2006). An asterisk indicates those species for which published record points were incorporated (see Materials and Methods). Endemic species are marked with a plus sign (+) for defining species and (++) for endemic but not defining AEs; not endemic characterizing species are marked with a numeral sign (#).

ORDER RODENTIA

Suborder Sciurognathi
Family Sciuridae – Subfamily Sciurinae – *Sciurus ignitus* #

Family Cricetidae – Subfamily Sigmodontinae – Tribe Akodontini – *A. albiventer* # – *A. aliquantulus* + – *A. boliviensis* # – *A. budini* # – *A. caenosus* # – *A. fumeus* # – *A. leucolimnaeus* + – *A. simulator* – *A. spegazzinii* – *A. sylvanus* ++ – *A. toba* # – *Necromys lactens* # – *N. lasiurus* # – *Oxymycterus paramensis* # – *O. wayku* ++

Family Cricetidae – Subfamily Sigmodontinae – Tribe Oryzomyini – *Euryoryzomys legatus* # – *Holochilus chacarius* – *Oligoryzomys chaoensis* # – *O. destructor*# – *O. cf O. flavescens* #

Family Cricetidae – Subfamily Sigmodontinae – Tribe Phyllotini – *Andalgalomys olrogi* # – *Auliscomys sublimis* # – *C. fecundus* – *C. laucha* – *C. lepidus* # – *C. musculinus* – *Eligmodontia bolsonensis* + – *E. hirtipes* # – *E. marica* – *E. moreni* # – *E. puerulus* # – *Graomys chacoensis* – *G. domorum* # – *G. griseoflavus* – *Phyllotis alisosiensis* + – *P. anitae* + – *P. caprinus* # – *P. osilae* – *P. xanthopygus* – *Salinomys delicatus* # – *Tapecomys primus* # – *T. wolffsohni* #

Family Cricetidae – Subfamily Sigmodontinae – Tribe Reithrodontini – *Reithrodon auritus* #

Family Cricetidae – Subfamily Sigmodontinae – Tribe Thomasomyini – *Rhipidomys austrinus* #

Family Cricetidae – Subfamily Sigmodontinae – Tribe Abrothricini – *Abrothrix andina* # – *A. illutea* + – *A. jelskii* #

Family Cricetidae – Subfamily Sigmodontinae – Incertae sedis – *Andinomys edax* # – *Neotomys ebriosus* #

Suborder Histricognathi
Family Erethizontidae – Subfamily Erethizontinae – *Coendou bicolor* * # – *C. prehensilis* * #

Family Chinchillidae – Subfamily Chinchillinae – *Chinchilla brevicaudata* * – *Lagidium viscacia* * #

Family Chinchillidae – Subfamily Lagostominae – *Lagostomus maximus* *

Family Caviidae – Subfamily Caviinae – *Cavia tschudii* – *Galea musteloides* – *Microcavia australis* – *M. shiptoni* * +

Family Caviidae – Subfamily Dolichotinae – *Pediolagus salinicola* *

Family Hydrochoeridae – Subfamily Hydrochoerinae – *Hydrochoerus hydrochaeris* * #

Family Dasyproctidae – *Dasyprocta punctata* * #

Superfamilia Octodontoidea – Family Ctenomyidae – *Ctenomys budini* + – *C. coludo* ++ – *C. juris* ++- *C. knighti* + – *C. latro* + – *C. occultus* ++ – *C. opimus* * # – *C. saltarius* + – *C. scagliai* + – *C. sylvanus* + – *C. tuconax* + – *C. tucumanus* + – *C. viperinus* +

Family Octodontidae – *Octodontomys gliroides* * – *Pipanacoctomys aureus* +

Family Abrocomidae – *Abrocoma cinerea* * #

Family Myocastoridae – *Myocastor coypus* *

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Acronyms of museum specimens identified to specific level by the authors and included in the analysis.