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Original Investigation

Scaling coexistence and assemblage patterns of desert small mammals

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ABSTRACT

Scaling biodiversity patterns has been recognized lately as a very important issue in the search of global processes; however coexistence and assemblage patterns are typically approached at a single spatial scale. Here, we examined coexistence and co-occurrence patterns of desert small mammal communities across different spatial scales in the search of general community patterns. We sampled small mammals in Monte desert (Argentina, South America) for small spatial scales and reviewed published papers from other worldwide deserts for large spatial scale analyses. We used classic community estimators (Shannon, Richness), rank abundance curves and fitting distributions to analyze species coexistence and co-occurrence patterns. Assemblage patterns were analyzed evaluating nestedness across spatial scales and among deserts. Worldwide desert small mammal assemblages are characterized mainly by low species richness and high variation in species composition. The central Monte desert of Argentina showed a consistent assemblage pattern across spatial scales, with a generalist species being the most abundant and widely distributed, accompanied by other subordinate and more narrowly distributed species. All Monte desert communities were significantly nested, with nestedness increasing with scale from patch to regional. Assemblage and coexistence patterns were similar when comparing worldwide deserts despite differences in total richness and faunal singularity. The degree of nestedness varied among worldwide deserts; however all of them showed a consistent nested pattern. Differences in the degree of nestedness could be a result of different regulating factors depending on the desert and scale. These results highlight the importance of including multiscale approaches when dealing with processes that structure desert communities.

Introduction

What allows species to coexist? Are there global assembly patterns? These are two of the most discussed topics in community ecology over the last four decades (Weiher and Keddy 2001). Nevertheless, because local assemblages are not isolated from, but are a subset of the regional biota, scaling biodiversity from local to regional scales is essential when trying to understand these two questions (Storch et al. 2007). Moreover, different processes that regulate assembly patterns usually act at different levels of spatial or temporal scales (Chandy et al. 2006; Kneitel and Chase 2004; Rodríguez and Ojeda 2011; Willig et al. 2003; Willis and Whittaker 2002). Therefore, the variables that account for species richness on small scales (spatial or temporal) may not be the same as those for large scales (Willig et al. 2003; Willis and Whittaker 2002).

Recently, one of the most studied community patterns is the nested subset pattern. A nested community pattern occurs when species assemblages on poorer sites are comprised of a subset of the species that occur at successively richer sites (Darlongton 1957; Patterson and Atmar 1986). Because of this, the ubiquitous distributed species are found everywhere, whereas the marginally distributed species occur only at the richest sites (Patterson and Atmar 1986). Different factors have been proposed to explain the nested pattern and they can be classified into two general groups: exogenous and endogenous factors. Exogenous factors include hypotheses such as habitat heterogeneity, nested habitats, environmental harshness and climatic variability (Ulrich et al. 2009 and references therein). Among the endogenous factors, interspecific interactions, mainly competition and mutualism, and niche packing have been proposed as the major regulating factors driving assemblage patterns (Kelt et al. 1999; Patterson and Brown 1991; Ulrich et al. 2009 and references therein).

When trying to understand general community patterns, e.g., nestedness, it is important to assess community structure at multiple spatial scales (Patterson and Brown 1991) mainly because regulating processes (such as habitat heterogeneity and interspecific interactions) are spatially variable. Nevertheless, to our knowledge there is no published research dealing with nested patterns across spatial scales, maybe due to the lack of current consensus on which nestedness metric to use (Ulrich et al. 2009) and/or

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the spatial scale at which nestedness should be analyzed (Patterson and Brown 1991).

Over the last 40 years, desert small mammals have been used as an excellent model in community ecology, mainly because assemblages are simple but diverse, and species are conspicuous and abundant (Shenbrot et al. 1999). Community structure of desert small mammals has been evaluated locally and regionally in a variety of deserts of America (Brown 1975; Brown and Kurzius 1987; Corbalán 2004; Fox and Brown 1993; Kelt 2011; Marquet 1994; Ojeda et al. 2011), Africa (Abu Baker and Patterson 2010, 2011), Australia (Fox 1987, 2011; Haythornthwaite and Dickman 2006; Morton et al. 1994) and Asia (Rogovin and Shenbrot 1995), as well as across continents (Kelt et al. 1996, 1999; Ojeda et al. 2000). Particularly, desert small mammals show nestedness of coexistence at local (Abu Baker and Patterson 2011; Kelt et al. 1999; Wang et al. 2010) and regional scales (Patterson and Brown 1991), meaning that assemblages on species-poor sites are often a subset of assemblages from species-rich sites (Patterson and Atmar 1986).

In South America, the diversity of Monte desert small mammals shows an irregular pattern across spatial scales, indicating that different processes operate at different spatial scales when structuring desert assemblages (Rodríguez and Ojeda 2011). Therefore, comparisons of different assemblage patterns across different spatial scales could shed light on general community patterns and their potential regulating processes. In this sense, understanding nestedness is essential when searching for overall community patterns not only in the Monte desert small mammal assemblages, but also in those occurring in deserts worldwide (Patterson and Brown 1991).

The general aim of our paper is to compare community patterns of desert small mammals across spatial scales, from patch to continental. Small mammal assemblages of the Monte desert were studied for small scale analyses (habitat patch, locality and regional) (Fig. 1) desert small mammal assemblages worldwide were compared for large scale analyses. In particular, we posed the following questions: (a) how do species coexistence patterns of Monte desert small mammals vary across spatial scales? (b) How do assemblage patterns (nestedness) vary across spatial scales? (c) Is there a general small mammal coexistence pattern across world deserts, if so, how is the pattern? We expect to find similar coexistence patterns across spatial scales, with dominant generalist species and other subordinate ones, and to find a nested structure across spatial scales.

Material and methods

We compared assemblage patterns at four spatial scales: patch, locality, region and continent. We used small mammal assemblages of the central Monte desert, Argentina, for analyzing coexistence and assemblage patterns at the smallest spatial scales, and published information on small mammal assemblage patterns around the world for the continental scale.

Study area and sampling design from patch to regional scale

In the Monte desert, the climate is arid to semi-arid and markedly seasonal with warm, rainy summers and cold, dry winters. Average annual rainfall varies along the latitudinal gradient from 50 mm in the north to 450 mm in the southeast. Mean temperature varies from <10 °C in winter to >20 °C in summer. Habitat heterogeneity and patchiness are major features of the Monte desert (Morello 1958). Six habitat types are present in the study area: *Prosopis* woodlands, *Larrea* shrublands, shrublands (other than *Larrea*), sand dunes, salt flats and pampas grasslands (Morello 1958).

Small mammal assemblage patterns were quantified along a 5° latitudinal range in Mendoza Province (from 32° to 37° south latitude) at three spatial scales: habitat patch, locality and regional (Fig. 1). Regional assemblage patterns were quantified along the central part of the Monte desert (96,000 km^2) (Fig. 1). This area was partitioned into six divisions along an aridity gradient (precipitation gradient) (n = 6, 16,000 km^2 each). Two to four localities were selected in each aridity division, 18 in all. Each locality included a total area of 2–3 ha and was separated from other localities by at least 60 km. Two to four different habitat patches were selected within each locality (n = 51). We selected habitat patches according to the classification of habitat types proposed by Morello (1958), and sampled all habitat types inside each locality. The limits between patches were ecological ones. Habitat patches were located 2–15 km apart and comprised 0.6 ha each. The lowest scaling level included 6 band transects (4 m × 250 m = 0.1 ha) at least 500 m apart (n = 306) (Fig. 1). Because of the hierarchical approach of this design, we provide a detailed description of each component of scales for each spatial scale. We followed the terminology and concepts of Scheiner et al. (2000). Sample extent (geographical space where comparisons are made) was the landscape encompassed by the central portion of the Monte biome and remained constant throughout all spatial scales. Sample grain (size of sample unit) and sample focus (area of inference) changed with scale as follows, but remained the same inside each scale: at the habitat patch scale focus and grain were 0.6 ha; at the locality scale they were 2–3 ha and at the regional scale they were 16,000 km^2.

Small mammal sampling

Trapping was performed between September 2005 and June 2008, and total sampling effort consisted of 23,000 trap/nights. Our sampling effort was focused between January and June of each year because small mammals of the Monte desert have their highest abundance at some point during this period (middle of summer through autumn in the Southern Hemisphere) (Corbalán and Ojeda 2004; Ojeda et al. 2011). In order to include and control temporal variability and improve the sampling design, we also sampled in other seasons on randomly scattered sampling localities between aridity ranges. For detailed sampling dates please see Appendix S1 in Supporting Information. Small mammal sampling was conducted with live-capture Sherman traps (27.5 cm × 8 cm × 9 cm.). Twenty five traps (10 m apart) were placed along a line transect on each band transect, and the system was kept active during three consecutive nights. Traps were baited with rolled oats and peanut butter and checked every morning. Captured animals were identified to species level, marked with picric acid for individual identification and then released. Small mammal sampling procedures and techniques were approved by the Dirección Provincial de Fauna de la Provincia de Mendoza.

Cross-continental community patterns (comparison among deserts)

For continental scale analyses, we used bibliographical reports from Atacama, Great Basin, Mojave, Sonoran, Chihuahuan, Australian and Egypt deserts, as well as sampling data from the Monte desert (see Table 1 for bibliographical and sampling details). Relative frequency was used to compare co-existence patterns among deserts since the number of sampled sites was different for each desert.

Data analysis

To describe general community characteristics, we estimate the media and standard deviation of species richness and diversity

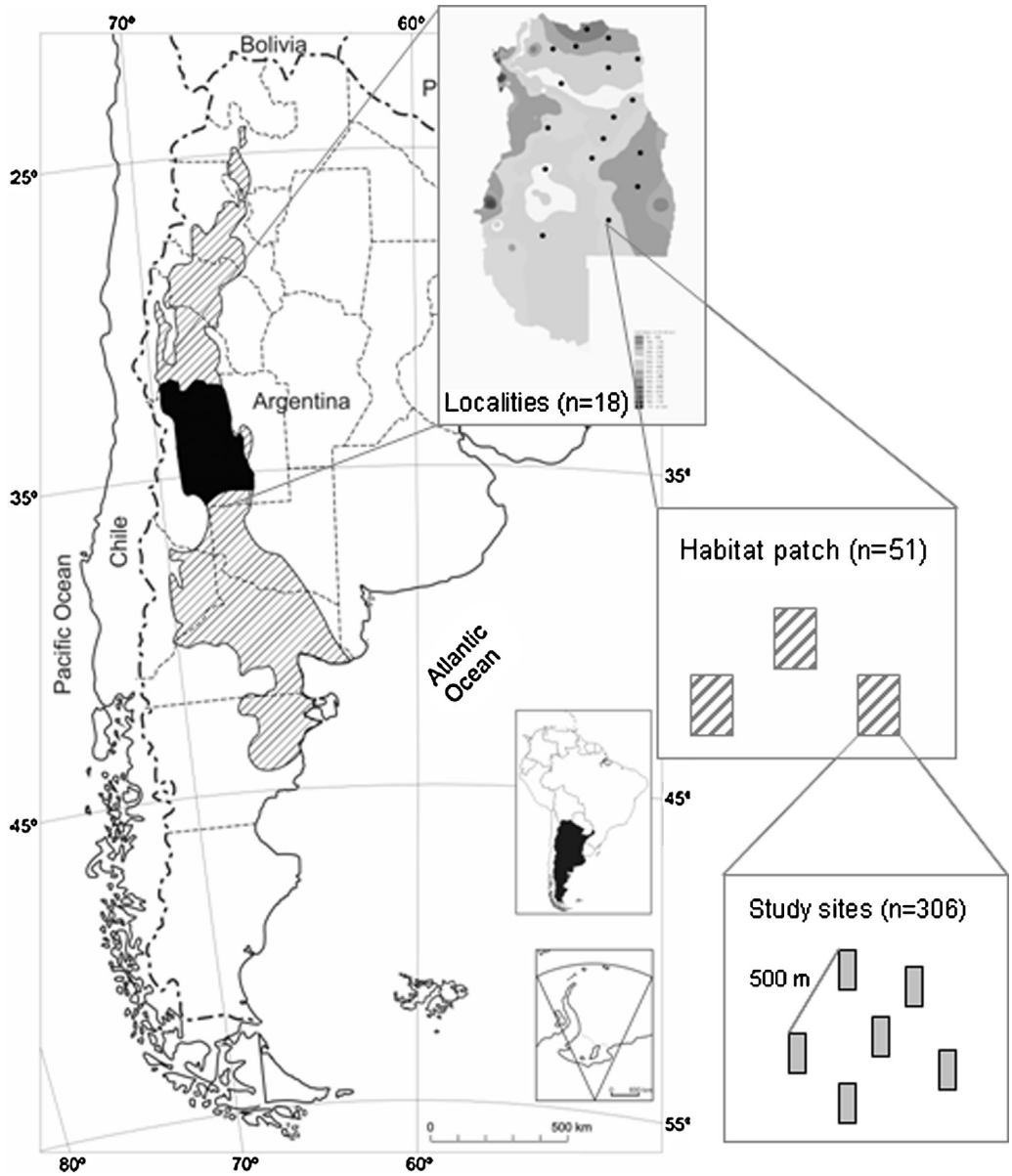

Fig. 1. Map of the study area and spatial design in the Monte desert, Argentina.

(Shannon index). Basic graphical and statistical analyses were used to analyze species coexistence and co-occurrence patterns at the patch scale. Species richness and abundance at the patch scale was estimated as the total species number (and abundance) of the six transects line. bB fitting data to a Poisson distribution, we assessed (1) the number of habitat patches containing assemblages with different species richness, and (2) the number of different species combinations in each assemblage (Magurran 2004). We also analyzed the co-occurrence frequencies of the most abundant species. We used a Chi-squared test to evaluate statistical differences in their patterns of coexistence with other species of the assemblage. Co-occurrence patterns were analyzed at local and regional scales using rank-abundance curves (Whittaker 1972; Feinsinger 2004).

Assemblage patterns with species co-occurrence within each scale were analyzed by estimating nestedness of species aggregation using two different nestedness metrics: temperature and WNODF. The temperature (T°) of the assemblage matrix

Table 1
Summary table of papers included in the among-deserts comparison.

Reference	Methodology (sampling years)	Minimum sample effort	Number and name of deserts included	Country	# Sites	# Species	# Combinations
Brown and Kurzius (1987)	Bibliography (1945–1982)	100 Trap/night	4 (Great Basin, Mojave, Sonora, Chihuahua)	United States	201	41	158
Morton et al. (1994)	Bibliography (1984–1993)	100 Trap/night	Not specified	Australia	245	26	108
Marquet (1994)	Bibliography (1945–1987)	Not specified	1 (Atacama)	Chile	120	18	63
Abu Baker and Patterson (2011)	Museum (1946–1982)	–	Not specified	Egypt	308	29	214
This work	Trapping (2005–2008)	450 Trap/night	1 (Monte)	Argentine	51	12	23

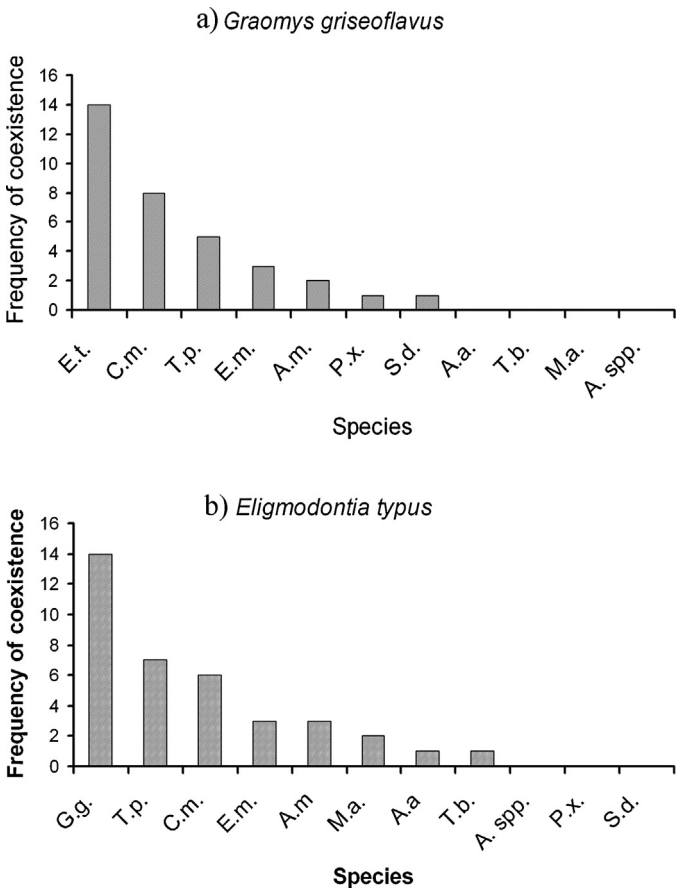

Fig. 2. Absolute frequency of co-occurrence patterns of most abundant species of small mammals of the Monte desert: (a) *Graomys griseoflavus* and (b) *Eligmodontia typus*. G.g: *Graomys griseoflavus*, E.t.: *Eligmodontia typus*, T.p.: *Thyllamys pallidior*, C.m.: *Calomys musculinus*, E.m.: *Eligmodontia moreni*, A.m.: *Akodon molinae*, M.a.: *Microcavia australis*, A.a.: *Abrotrixs andinus*, T.b.: *Tympanoctomys barrerae*, A.spp.: *Akodon* spp. P.x.: *Phyllotis xanthopygus*, S.d.: *Salinomys delicatus*.

(species × site) was calculated using BINMATNEST software (Rodríguez-Gironés and Santamaría 2006), with the temperature formula proposed by Atmar and Patterson (1993) which only uses richness values. Temperature is a measure of matrix disorder and ranges from 0° ("cold", perfect order or absolute nestedness) to 100° ("hot", minimal nestedness or perfect checkboard) (Patterson et al. 2009). Observed and expected values of T° were compared by running the program with 1000 iterations (bootstrapping) and testing the statistical significance of the observed values. Although the T° metric does not allow comparisons if they differ in size and fill (Ulrich et al. 2009) the temperature metric has been historically used to compute nestedness and so we included it in this paper.

The WNODF metric was calculated using NODF software (Almeida-Neto and Ulrich 2011). The NODF program allows estimating NODF and WNODF metrics, which have three advantages over T°: they (a) include abundance information when computing nestedness, (b) are not affected by either size or fill and (c) separates the effect of species incidence from that of species composition (Ulrich et al. 2009). The segregation of species incidence and species composition allows us to hypothesize about the nature of regulating factors (Almeida-Neto et al. 2008). If the WNODFr statistic (species incidence) is significantly different from the null model, then differences in environmental variables are supposed to generate nested patterns. On the other hand, if WNODFc statistic (species composition) is significantly different from the null model, then assemblage patterns are caused mainly by life history traits (Ulrich et al. 2009). When analyzing abundance matrices we used the following parameters: abundance null model = resampling with fixed row and column weights (maintains the original matrix size and the original abundance in both rows and columns); matrix packing = according to species richness and abundance. Observed and expected values of NODF and WNODF were compared by running the program with 1000 iterations (bootstrapping) and testing the statistical significance of the observed values. The NODF program also allows us to estimate the NODF statistic. This parameter is estimated in the same way as the WNODF but only includes richness values (Almeida-Neto and Ulrich 2011). Because abundance data are usually difficult to obtain, we also report the NODF statistics and p values for comparisons with future studies. To test whether assemblage patterns were consistent across spatial scales, we compared NODF and WNODF values across spatial scales.

At the continental scale (among-deserts), we compared coexistence patterns by plotting the number of sites containing assemblages with different species richness in each desert, as well as the number of different species combinations within each assemblage. We fitted each distributional curve of species number per site to a Poisson distribution. We compared nestedness structure of small mammal assemblages only between Monte (results of this paper) and Egyptian deserts (data from Abu Baker and Patterson 2011) using the NODF metric, because previous papers do not use this metric. We used two spatial scales: regional and patch. For Egyptian data we used the NODF value of the 335 Egyptian assemblages for the patch scale, and the NODF value estimated from assemblages of the North region, reported on Table 3 of Abu Baker and Patterson (2011).

Results

We captured a total of 441 individuals (in 534 capture events) representing 12 species. We recorded 3 rodent families and one marsupial. Among rodents, species captured were: (1) Cricetidae: *Eligmodontia typus*, *Eligmodontia moreni*, *Graomys griseoflavus*, *Calomys musculinus*, *Phyllotis xanthopygus*, *Akodon molinae*, *Akodon sp.*, *Abrothrix andinus*, *Salinomys delicatus*, (2) Caviidae: *Microcavia australis*, and (3) Octodontidae: *Tympanoctomys barrerae*. The only marsupial species was *Thylamys pallidior*. These species represent 65% of the total Monte desert small mammal richness (Ojeda and Tabeni 2009). Capture success was 2.6%. All scientific names follow the nomenclatural authority of Barquez et al. (2006).

Assemblage and coexistence patterns at the patch scale

Species richness at the patch scale ranged from one to five species. Mean species richness was two, with a standard deviation of 1.3. Number of captured individuals also varied between patches, ranging from zero (on seven from 53 sites) to 40. Mean number of individuals was 8 per patch, and standard deviation (SD) was 8.7. Diversity varied between patches from 0 to 1.49. Mean diversity was 0.51 and SD was 0.44. For detailed values of each patch please see S1 in Supporting Information.

More than 70% of the patches were composed of one to three species. Number of species per sites was fitted to a Poisson distribution ($G = 1.82$; $p = 0.95$), with most sites composed of few species and few sites with several species. We found 23 different species combinations of small mammal assemblages at the patch scale. The highest number of combinations was of two species, followed by patches with 3 species. Number of combinations per species number showed a Poisson distribution ($G = 2.39$; $p = 0.255$), with most combinations at sites with two-three species.

The most abundant species were *Graomys griseoflavus* and *Eligmodontia typus*. Both species coexisted more frequently with each

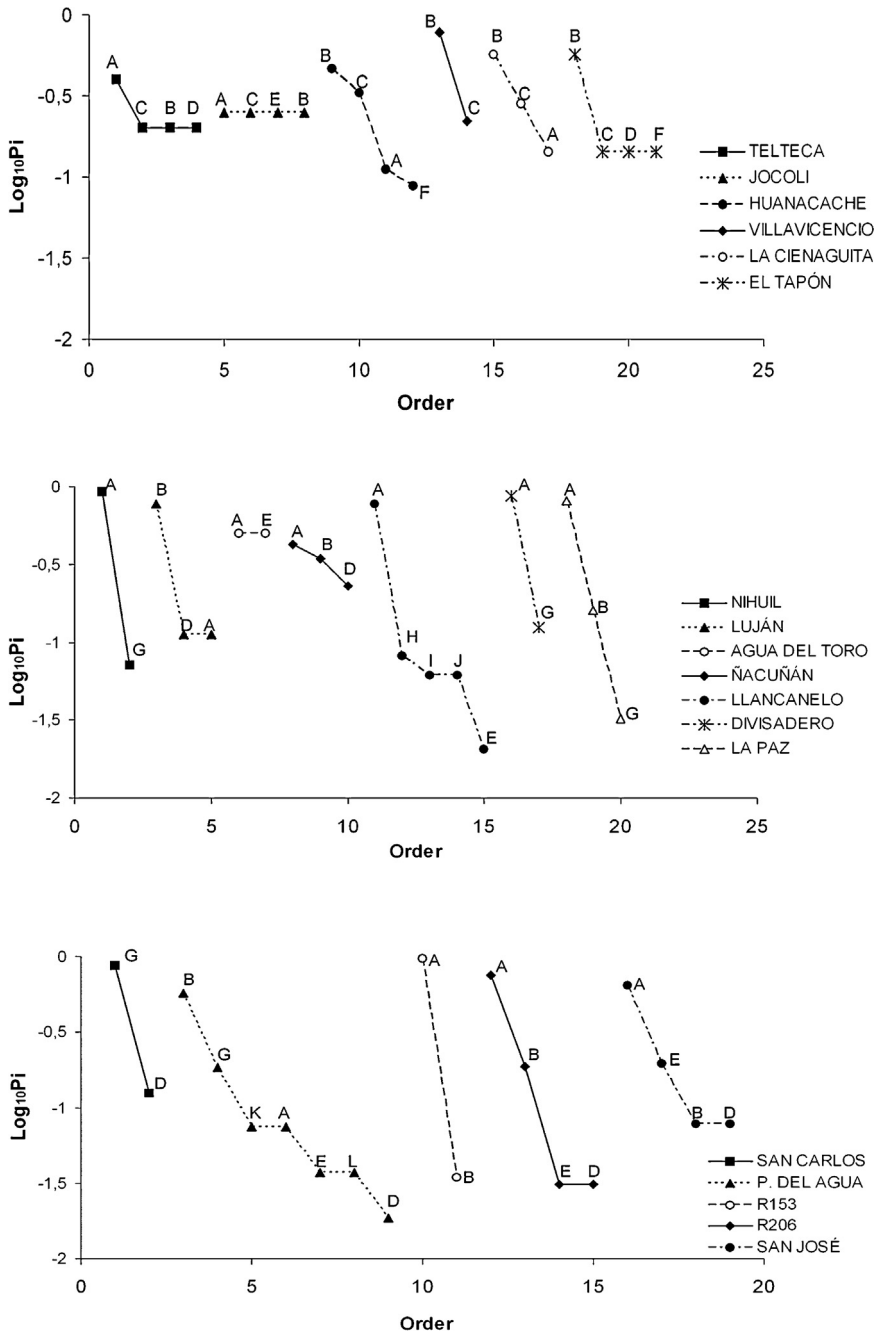

Fig. 3. Rank-abundance curves per locality (listed on the right side) in the Monte desert. Log 10PI represents the logarithm on base 10 of the relative abundance of each species on each locality. A: *E. typus*, B: *G. griseoflavus*, C: *E. moreni*, D: *C. musculinus*, E: *T. pallidior*, F: *S. delicatus*, G: *A. molinae*, H: *A. andinus*, I: *T. barrerae*, J: *M. australis*, K: *Akodon* spp.

other than with the others. *G. griseoflavus* was recorded in 25 of the 53 patches, either alone ($n = 4$) or with other species ($n = 21$). *G. griseoflavus* was found in 12 different species combinations, with *E. typus* and *C. musculinus* being the common species ($\chi^2 = 28.52$; $p < 0.01$; df = 7) (Fig. 2a). *E. typus* was recorded in 28 of the 53 sampled assemblages, either alone ($n = 7$) or with other species ($n = 21$). *E. typus* was found in 14 different assemblage combinations, coexisting more frequently with *G. griseoflavus*, *T. pallidior* and *C. musculinus* than with the others ($\chi^2 = 28.40$; $p < 0.01$; df = 7) (Fig. 2b). This pattern of species occurring more frequently with a few species and less frequently with a large number of species also occurred with other species. Coexistence between congeneric species of *Eligmodontia* was recorded only in 3 of 53 patches. Neither species of *Eligmodontia* occurred alone, but were accompanied by *G. griseoflavus*, and in one case also by the marsupial *T. pallidior*.

Species combinations and coexistence at the locality scale

All localities differed in their assemblage constitution, and richness varied between two and six species. At the locality scale, there was a common pattern of assemblages with a more abundant species and subordinate ones (Fig. 3). Core-satellite species, independently of the locality or the precipitation range considered, were always *E. typus* or *G. griseoflavus*, except in San Carlos locality where *A. molinae* was the dominant species. *G. griseoflavus*

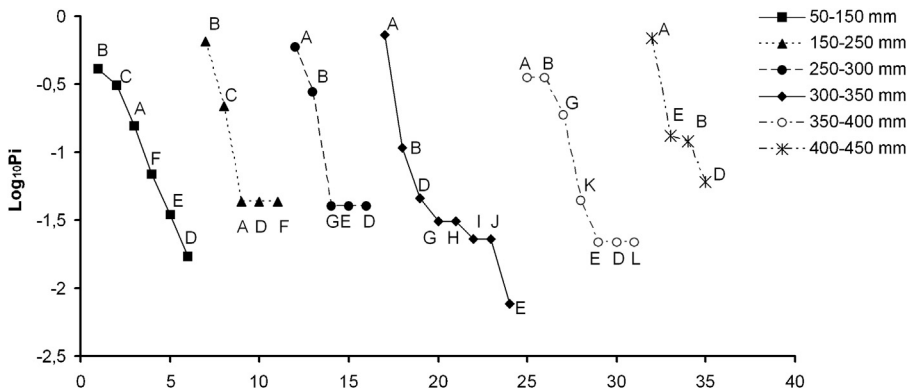

Fig. 4. Rank-abundance curves per precipitation range in the Monte desert. Values correspond to the Simpson's index. A: *E. typus*, B: *G. griseoflavus*, C: *E. moreni*, D: *C. musculinus*, E: *T. pallidior*, F: *S. delicatus*, G: *A. molinae*, H: *A. andinus*, I: *T. barrerae*, J: *M. australis*, K: *Akodon* spp.

was exclusively dominant in all localities within the precipitation range between 150 and 200 mm, whereas *E. typus* was exclusively dominant in 300–350 and 400–450 precipitation ranges (Fig. 3). Assemblages in the other precipitation ranges varied in dominant species.

Assemblage patterns at the regional scale: the Monte desert

Rank-abundance curves showed a clear assemblage pattern in small mammals of the Monte desert (Fig. 4). Species richness varied between four and eight depending on precipitation, with the intermediate range (300–350 mm precipitation) being richer and the wetter range (400–450 mm precipitation) being poorer. As at the other spatial scales, there was a clear pattern of a dominant species (*E. typus* or *G. griseoflavus*) and subordinates.

Phyllotis xanthopygus and *Akodon* sp. were only found in intermediate precipitation ranges (350–400 mm) and *Salinomys delicatus* was only recorded in extremely arid regions (50–250 mm). *Calomys musculinus*, *Eligmodontia typus* and *Graomys griseoflavus* were the only three species recorded along the whole precipitation range analyzed (Fig. 4).

Nested patterns across spatial scales in the Monte desert

We found significantly low values for temperature at all spatial scales [$T^{\circ}_{(patch)} = 6.18$, $p < 0.0001$; $T^{\circ}_{(local)} = 16.47$, $p = 0.033$; $T^{\circ}_{(regional)} = 16.44$, $p = 0.033$], indicating a nested pattern in the small mammal assembalges of the Monte desert. When analyzing the NODF and WNODF metrics at the patch and local scales we found that assemblages were significantly nested (Table 2). Species incidence and species composition were also significantly nested at both special scales and for both estimators (Table 2). At the regional scale, both NODF and WNODF showed significant differences compared to the null model, indicating that small mammals of Monte desert were significantly nested (Table 2). When analyzing species incidence and species composition separately, we found no significant differences in species incidence at the regional scale, for either NODFc or WNODFc (Table 2). Finally, when comparing values of NODF and WNODF across spatial scales, we found that nestedness increased from patch to regional scale.

Comparisons among worldwide deserts

Small mammals showed similar patterns of species coexistence across deserts (Fig. 5). The frequency of number of species per sampling unit had mean values of around 2–3 species. Mean values for North America was 3 species per site, 2.64 for Australia, 2.78 for Egypt, 3 for Atacama and 2 for the Monte desert. Despite the

Table 2
Results of nestedness analyses for the Monte desert assemblages. NODF = general nestedness estimator of species richness (does not includes abundance), WNODF = general nestedness estimator of species diversity (richness + abundance), NODFc and WNODFc = column nestedness estimator of species diversity or richness (species composition), NODFr and WNODFr = row nestedness estimator of species diversity or richness (species incidence).

Scale	Metric	Observed	Expected	*Z*	*p*
Regional	WNODF	37.60	55.03	−3.61	<0.0001
	WNODFc	44.13	55.52	−1.25	0.106
	WNODFr	36.11	55.77	−4.23	<0.0001
	NODF	62.71	74.47	−2.53	0.003
	NODFc	78.65	78.63	0.02	0.4984
	NODFr	59.09	73.83	−3.14	0.0004
Local	WNODF	22.56	47.05	−5.71	<0.0001
	WNODFc	22.79	48.32	−5.09	<0.0001
	WNODFr	22.04	45.03	−6.03	<0.0001
	NODF	46.81	71.06	−5.46	<0.0001
	NODFc	49.06	73.08	−5.01	<0.0001
	NODFr	41.57	66.36	−5.38	<0.0001
Patch	WNODF	16.00	27.14	−4.22	<0.0001
	WNODFc	15.91	26.95	−4.11	<0.0001
	WNODFr	17.66	31.18	−4.08	<0.0001
	NODF	31.47	43.75	−4.37	<0.0001
	NODFc	31.42	43.35	−4.25	<0.0001
	NODFr	32.44	51.08	−4.33	<0.0001

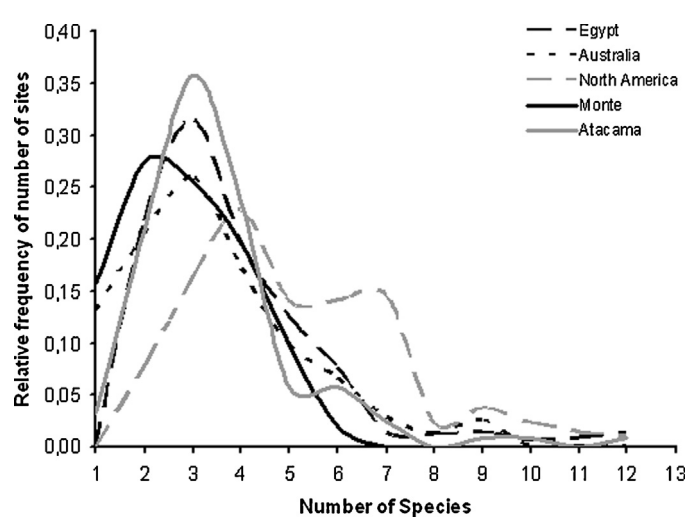

Fig. 5. Number of sites as a function of assemblage sites (number of species per site) for five deserts: North American, Australian, Egyptian, Atacama and Monte.

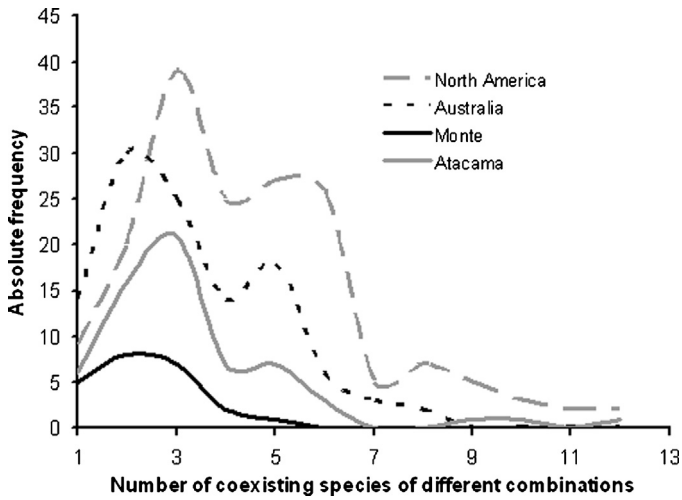

Fig. 6. Number of combinations as a function of species richness for North American, Atacama, Australian and Monte deserts.

fact that the mean number of species was similar among deserts, there was a marked difference in total species richness, with the North American deserts being the richest and the Monte desert the poorest (Table 1).

In terms of species identity, we found that North American, Australian and Atacama deserts have 2 peaks of species combinations, with most combinations occurring with 3–5 species per site. In the Monte desert, however, there was only 1 peak combination with 2 species per site (Fig. 6).

When comparing nestedness of Egyptian and Monte desert small mammal assemblages, at the regional scale, we found that Monte desert assemblages were more nested than Egyptian ones ($NODF_{(Egyptian)} = 19.32–29.71$; $NODF_{(Monte)} = 62.71$), with NODFr representing the most dimension of variation for both deserts. We found the same general pattern at the patch scale, with the Monte desert being more nested than the Egyptian desert ($NODF_{(Egyptian)} = 19.97$; $NODF_{(Monte)} = 31.47$). NODFr was also the more explicative metric of NODF for both deserts.

Discussion

This is the first study that investigates the way in which desert small mammal assemblage and coexistence patterns vary among spatial scales. Worldwide desert small mammals assemblages are characterized mainly by low species richness and high variation in species composition. We found a consistent assemblage pattern across spatial scales for the central Monte desert, with a generalist species being the most abundant and widely distributed, accompanied by other subordinate and more narrowly distributed species. Richer sites tended to include species present on poorer sites, indicating a nested pattern. The poorest assemblages were mainly constituted by widely distributed species, whereas the richest ones were composed of widely distributed species accompanied by other species with narrow distribution. Nestedness increased with scale from patch to regional inside the Monte desert. When comparing worldwide deserts, assemblage and coexistence patterns were similar despite differences in total richness and faunal singularity. Finally, all deserts showed a consistent nested pattern, although degree of nestedness varied among them.

Coexistence and assemblage patterns across spatial scales on Monte desert

Most assemblages consist of just one to three species, with a total of 12 species recorded and 23 different combinations. Such results could be related to small mammal habitat preferences, and indicate that a few species are habitat generalists and therefore widely distributed, while specialists are less abundant or marginally distributed, as proposed by Brown (1984). These recorded assemblage patterns were expected from niche theory and reflects the capacity of local patches to fulfill the individual niche requirements of all the different species (Brown and Kurzius 1987).

Similar patterns of “generalist species” being the more widely distributed ones were also recorded for other small mammals' assemblage deserts (Abu Baker and Patterson 2011; Coppeto et al. 2006; Haythornthwaite and Dickman 2006; Rogovin and Shenbrot 1995). Body mass, trophic structure and habitat heterogeneity are the driving forces that generate these patterns in Australia, Egypt and North American (Morton et al. 1994; Abu Baker and Patterson 2010; Kelt 2011; Fox 2011). In the Monte desert, *E. typus* and *G. griseoflavus* are habitat generalists and have wide geographic ranges (Lanzone 2009; Suárez 2007). *E. typus* prefers open habitats such as sand dunes or grassed systems (Corbalán and Debandi 2006; Corbalán et al. 2006) and is omnivorous (Giannoni et al. 2005), meanwhile *G. griseoflavus* inhabits a wide variety of habitats (Corbalán et al. 2006; Gonnet and Ojeda 1998; Tabeni and Ojeda 2005) and is herbivorous (Giannoni et al. 2005).

In Egypt and Australia, high levels of aridity and low habitat heterogeneity seem to promote higher number of sites with low-richness (Abu Baker and Patterson 2011). Nevertheless this is not the case of the Monte desert, where high habitat heterogeneity is one of its major characteristics (Morello 1958). In contrast, species specialization and endemisms seem to be the distinctive feature sof Monte desert (Ojeda et al. 2000) and the possible cause of the low number of combinations and high number of sites with low-richness (Table 1, Fig. 5). *S. delicatus* and *T. barrerae* (two of the 12 recorded species) are an example of this, being habitat and diet specialists, with a narrow distribution in central desert of Argentina (Rodríguez et al. 2012; Ojeda et al. 1996; Ojeda et al. 2007)

In the Monte desert, larger spatial scale analyses (locality and regional) showed the same assemblage (generalists being the commonest species) and co-occurrence (nestedness) patterns as the smaller spatial scale. All metrics used to estimate nestedness (temperature, NODF and WNODF) yielded the same pattern of significant nestedness at the three spatial scales. This pattern was corroborated by rank-abundance curves, where generalist species were recorded in most assemblages and were the most abundant, while specialist species were restricted to only some assemblages and were less abundant.

Partitioning the NODF and WNODF metrics allowed us to evaluate the different potential factors driving different degrees of nestedness across spatial scales. At the smallest spatial scale (habitat patch) species incidence and species composition were significantly nested, so both interspecific interactions and environmental characteristics could be driving the pattern of species coexistence. This result supports previous research on small mammal communities of Monte desert (Albanese et al. 2011; Campos et al. 2001; Corbalán and Ojeda 2004; Corbalán et al. 2006; Giannoni et al. 2005; Gonnet and Ojeda 1998; Tabeni and Ojeda 2005; Tabeni et al. 2007).

At the regional scale, nestedness of Monte desert small mammal assemblages was mostly driven by species incidence, with species composition not being explicative. The lack of nestedness of species incidence at the regional scale could imply that environmental factors, such as precipitation and productivity, could be the major regulating factors at the expense of ecological interactions at higher spatial scales. According to Ulrich et al. (2009), because the design factor for regional scale was the precipitation gradient, we cannot separate mathematically the effect of the assemblage pattern from the effect of the design factor. Nevertheless, if the resulting

pattern is a consequence of the design factor (precipitation gradient) we would have expected to find a high-turnover pattern instead of a nested pattern for species composition, mainly because beta diversity (or species turnover) is more important than alfa at higher spatial scales (Rodríguez and Ojeda 2011).

Finally, we found that nestedness increased with spatial scale from patch to regional. This result could be explained by the hypothesis of passive sampling. This hypothesis is based on the power function relationship between richness and area (SAR), and predicts that species richness increases in higher spatial scales depending on the considered sampling area (Cutler 1994; Ulrich et al. 2009 and references therein). Nevertheless, other causes such as selective extinction and colonization rates in evolutionary times could also cause this pattern (Patterson and Brown 1991).

Coexistence and assemblage patterns among worldwide desert

When comparing patterns of coexistence of small mammals across deserts worldwide, we found similar mean values of richness of 2–3 species per site, but marked differences in total species richness. North American deserts can be considered an "outlier", with some assemblages being constituted of more than 7 species (Brown and Kurzius 1987; Fig. 5). Nevertheless, for all deserts, when considering species combinations, we found that most combinations were recorded for assemblages constituted by 2 or 3 species (Fig. 6).

We did find differences when fitting a Poisson distribution between deserts. North American, Australian and Atacama deserts showed small mammal assemblage patterns different from random ($G = 20.9$; $p < 0.05$ in North America; $G = 15.4$, $p < 0.025$ in Australia, $G = 76.44$, $p < 0.001$ in Atacama) (Brown and Kurzius 1987; Marquet 1994; Morton et al. 1994), meanwhile Monte desert small mammal assemblages were randomly distributed ($G = 2.39$; $p = 0.25$). This means that there are a high number of combinations with few species and few combinations with several species in North American, Australian and Atacama deserts; whereas in the Monte desert, this difference is not so clear. When comparing nestedness values among deserts, we found that Monte desert assemblages were more nested than the Sahara desert. This means that in the Monte desert, small mammal assemblages are constituted by more generalist and widely distributed species than the Sahara desert. This difference could be caused by an ecological response of biodiversity to nested habitats or by different tolerances of species to environmental extremes, or simply being a biogeographical response of regional species pools to historical events of colonization and/or extinction (Ulrich et al. 2009).

Final conclusions

In this study, we found that nestedness occurred at and across all spatial scales in desert small mammal assemblages. This result highlights the importance of scaling biodiversity and community patterns when trying to understand desert small mammal assemblages (Rodríguez and Ojeda 2011), and sheds light on the necessity of studies dealing with processes and regulating factors in and across a wide range of spatial scales. One of the major problems when dealing with macroecological patterns and processes is the lack of a clear specification of the grain and extent of scales (Rahbek 2005). Although each desert has its own evolutionary and biogeographic history, considered as a major cause of nestedness (Patterson and Brown 1991), it is hardly included in the macroecological approach. Differences in scale and species pool seem to also be the cause for the different points of view expressed by Kelt et al. (1999) and Ojeda et al. (2000) regarding the commonness or singularity of desert small mammal assemblages worldwide. Maybe it is because of this that the regulating factors are different, despite similar assemblage pattern among deserts (Meserve et al. 2011), reflecting the singularity of each desert biota. On the other hand, the proposed regulating factors could be associated with the scale (grain, extent and focus) considered in each study and the lack of a general regulatory mechanism is due to a problem of sampling design. Because scale should not be a problem when dealing with global patterns, it is necessary to specify more clearly the extent, grain and focus of the spatial scale so that assemblage patterns can be compared with more clarity. Finally, despite the difficulty of dealing with a multiscale approach, we encourage scientists to adopt a multifactorial view when analyzing assemblage structure and co-occurrence patterns and processes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2013.04.003.

References

Abu Baker, M., Patterson, B.D., 2010. Patterns in the local assembly of Egyptian rodent faunas: areography and species combinations. Mamm. Biol. 75, 510–522.
Abu Baker, M., Patterson, B.D., 2011. Patterns in the local assembly of Egyptian rodent faunas: co-occurrence and nestedness. J. Arid Environ. 75, 15–19.
Albanese, S., Rodríguez, D., Ojeda, R.A., 2011. Differential use of vertical space by small mammals in the Monte desert. Argent. J. Mammal. 93, 1270–1277.
Almeida-Neto, M., Guimarães, P., Guimarães Jr., P.R., Loyola, R.D., Ulrich, W., 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117, 1227–1239.
Almeida-Neto, M., Ulrich, W., 2011. A straightforward computational approach for measuring nestedness using quantitative matrices. Environ. Model. Softw. 26, 173–178.
Atmar, W., Patterson, B.D., 1993. The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia 96, 373–382.
Barquez, R.M., Díaz, M.M., Ojeda, R.A., 2006. Mamíferos de Argentina: Sistemática y distribución. SAREM, Tucumán, Argentina.
Brown, J.H., 1975. Geographical ecology of desert rodents. In: Cody, M.L., Diamond, J.M. (Eds.), Ecology and Evolution of Communities. Belknap Press, London, England, pp. 315–341.
Brown, J.H., 1984. On the relationship between abundance and distribution of species. Am. Nat. 124, 255–279.
Brown, J.H., Kurzius, M.A., 1987. Composition of desert rodent faunas: combinations of coexisting species. Ann. Zool. Fenn. 24, 227–237.
Campos, C.M., Ojeda, R.A., Monge, S., Dacar, M., 2001. Utilization of food resources by small and medium-sized mammals in the Monte Desert biome, Argentina. Aust. Ecol. 26, 142–149.
Chandy, S., Gibson, D.J., Robertson, P.A., 2006. Additive partitioning of diversity across hierarchical spatial scales in a forested landscape. J. Appl. Ecol. 43, 792–801.
Coppeto, S.A., Kelt, D.A., Van Vuren, D.H., Wilson, J.A., Bigelow, S., 2006. Habitat associations of small mammals at two spatial scales in the northern Sierra Nevada. J. Mammal. 87, 402–413.

Corbalán, V.E., 2004. Uso de hábitat y ecología poblacional de pequeños mamíferos del desierto del Monte central, Mendoza, Argentina. Universidad Nacional de La Plata, La Plata, Argentina (Doctoral Dissertation).
Corbalán, V., Ojeda, R.A., 2004. Spatial and temporal organisation of small mammal communities in the Monte desert. Argent. Mamm. 68, 5–14.
Corbalán, V., Debandi, G., 2006. Microhabitat use by *Eligmodontia* typus (Rodentia:Muridaae) in the Monte Desert (Argentina). Mamm. Biol. 71, 124–127.
Corbalán, V., Tabeni, S., Ojeda, R.A., 2006. Assessment of habitat quality for four small mammal species of the Monte Desert. Argent. Mamm. Biol. 71, 227–237.
Cutler, A.H., 1994. Nested biotas and biological conservation: metrics, mechanisms, and meaning of nestedness. Landscape Urban Plann. 28, 73–82.
Darlongton, P.J., 1957. Zoogeography: The Geographical Distribution of Animals. John Wiley, Hoboken, USA.
Feinsinger, P., 2004. El Diseño de Estudios de Campo Para la Conservación de la Biodiversidad. Editorial Fan Bolivia, Santa Cruz de la Sierra, Bolivia.
Fox, B.J., 1987. Species assembly and the evolution of community structure. Evol. Ecol. 1, 201–213.
Fox, B.J., Brown, J.H., 1993. Assembly rules for functional groups in North American desert rodent communities. Oikos 67, 358–370.
Fox, B.J., 2011. Review of small mammal trophic structure in drylands: resource availability, use, and disturbance. J. Mamm. 92, 1179–1192.
Giannoni, S.M., Borghi, C.E., Dacar, M.A., Campos, C.M., 2005. Main food categories in diet of Sigmodontine rodents in the Monte (Argentina). Mastozool. Neotrop. 12, 181–187.
Gonnet, J.M., Ojeda, R.A., 1998. Habitat use by small mammals in the arid Andean foothills of the Monte Desert of Mendoza, Argentina. J. Arid Environ. 38, 349–357.
Haythornthwaite, A.S., Dickman, C.R., 2006. Distributions, abundance, and individual strategies: a multi-scale analysis of dasyurid marsupials in arid central Australia. Ecography 29, 285–300.
Kelt, D.A., 2011. Comparative ecology of desert small mammals: a selective review of the past 30 years. J. Mammal. 92, 1158–1178.
Kelt, D.A., Brown, J.H., Heske, E.J., Marquet, P.A., Morton, S.R., Reid, J.R.W., Rogovin, K.A., Shenbrot, G., 1996. Community structure of desert small mammals: comparisons across four continents. Ecology 77, 746–761.
Kelt, D.A., Rogovin, K., Shenbrot, G., Brown, J.H., 1999. Patterns in the structure of Asian and North American desert small mammal communities. J. Biogeogr. 26, 825–841.
Kneitel, J.M., Chase, J.M., 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecol. Lett. 7, 69–80.
Lanzone, C., 2009. Sistemática y Evolución del Género Eligmodontia. Universidad Nacional de Córdoba, Córdoba, Argentina (Doctoral Dissertation).
Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Publishing, Oxford.
Marquet, P., 1994. Diversity of small mammals in the Pacific Coastal Desert of Peru and Chile and in the adjacent Andean area – biogeography and community structure. Aust. J. Zool. 42, 527–542.
Meserve, P.L., Dickman, C.R., Kelt, D.A., 2011. Small mammal community structure and dynamics in aridlands: overall patterns and contrasts with southern hemispheric systems. J. Mammal. 92, 1155–1157.
Morello, J., 1958. La provincia fitogeográfica del Monte. Opera Lilloana 2, 1–155.
Morton, S., Brown, J., Kelt, D., Reid, J., 1994. Comparisons of community structure among small mammals of North-American and Australian deserts. Aust. J. Zool. 42, 501–525.
Ojeda, A.A., Gallardo, M.H., Mondaca, F., Ojeda, R.A., 2007. Nuevos registros de *Tympanoctomys barrerae* (Rdenti, Octodontidae). Mastozool. Neotr. 14, 267–270.
Ojeda, R.A., Blendinger, P.G., Brandl, R., 2000. Mammals in South American drylands: faunal similarity and trophic structure. Global Ecol. Biogeogr. 9, 115–123.
Ojeda, R.A., Gonnet, J.M., Borghi, C.E., Giannoni, S.M., Campos, C.M., Díaz, G.B., 1996. Ecological observation of the red vizcacha rat *Tympanoctomys barrerae* in the desert habitats of Argentina. Mastozool. Neotrop. 3, 183–191.
Ojeda, R., Tabeni, S., 2009. The mammals of the Monte Desert revisited. J. Arid Environ. 73, 173–181.
Ojeda, R.A., Tabeni, S., Corbalán, V., 2011. Mammals of the Monte Desert: from regional to local assemblages. J. Mammal. 92, 1236–1244.
Patterson, B.D., Atmar, W., 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. Biol. J. Linn. Soc. 28, 65–82.
Patterson, B.D., Brown, J.H., 1991. Regionally nested patterns of species composition in granivorous rodent assemblages. J. Biogeogr. 18, 395–402.
Patterson, B.D., Dick, C.W., Dittmar, K., 2009. Nested distributions of bat flies (Diptera: Streblidae) on Neotropical bats: artifact and specificity in host–parasite studies. Ecography 32, 481–487.
Rahbek, C., 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecol. Lett. 8, 224–239.
Rodríguez, D., Ojeda, R.A., 2011. Patterns of diversity of the Monte desert small mammals across multiple spatial scales. J. Arid Environ. 75, 424–431.
Rodríguez, D., Lanzone, C., Chillo, V., Cuello, P., Albanese, S., Ojeda, A., Ojeda, R., 2012. Historia natural de un roedor raro del desierto argentino, *Salinomys delicatus* (Cricetidae, Sigmodontinae). Rev. Chil. His. Nat. 85, 13–27.
Rodríguez-Gironés, M.A., Santamaría, M.A., 2006. A new algorithm to calculate the nestedness temperature of presence–absence matrices. J. Biogeogr. 33, 924–935.
Rogovin, K., Shenbrot, G., 1995. Geographical ecology of Mongolian desert rodent communities. J. Biogeogr. 22, 111–128.
Scheiner, S.M., Cox, S.B., Willig, M., Mittelbach, G.G., Osenberg, C., Kaspari, M., 2000. Species richness, species – area curves and Simpson' s paradox. Evol. Ecol. Res. 2, 791–802.
Shenbrot, G.I., Krasnov, B.R., Rogovin, K.A., 1999. Spatial Ecology of Desert Rodent Communities. Springer, Berlin.
Storch, D., Marquet, P.A., Brown, J.H., 2007. Scaling Biodiversity. Cambridge University Press, Cambridge, UK.
Suárez, S.N., 2007. Estudios citogenéticas en Graomys grisoflavus (Rodentia, Muridae, Sigmodontinae). Universidad Nacional de Misiones, Misiones, Argentina (Licenciatura Dissertation).
Tabeni, M.S., Ojeda, R.A., 2005. Ecology of Monte desert small mammals in disturbed and undisturbed habitats. J. Arid Environ. 63, 244–255.
Tabeni, S., Mastrantonio, L., Ojeda, R.A., 2007. Linking small desert mammal distribution to habitat structure in a protected and grazed landscape of the Monte. Argent. Acta Oecol. 31, 259–269.
Ulrich, W., Almeida-Neto, M., Gotelli, N.J., 2009. A consumer's guide to nestedness analysis. Oikos 118, 3–17.
Wang, Y., Bao, Y., Yu, M., Xu, G., Ding, P., 2010. Nestedness for different reasons: the distributions of birds, lizards and small mammals on islands of an inundated lake. Divers. Distrib. 16, 862–873.
Weiher, E., Keddy, P., 2001. Ecological Assembly Rules. Cambridge University Press, UK.
Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21, 213–251.
Willig, M.R., Kaufman, D.M., Stevens, R.D., 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annu. Rev. Ecol. Evol. 34, 273–309.
Willis, K.J., Whittaker, R.J., 2002. Species diversity: scale matters. Science 295, 64–66.