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# Patterns of diversity of the Monte Desert small mammals across multiple spatial scales

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## ABSTRACT

The relationship between spatial scale and biodiversity patterns is a highly debated topic in ecology. We evaluated the partition of small mammal diversity at multiple spatial scales and analyzed protected areas in order to evaluate their role of protecting biodiversity at the regional scale. Diversity of small mammals in the Monte Desert was quantified at the regional biome scale (96,000 km$^2$) ($\gamma$) and partitioned at three spatial scales: aridity range ($\alpha_3, n = 6,16\ 000\ \text{km}^2$), locality level ($\alpha_2, n = 18, 2{-}3$ ha), and habitat patch ($\alpha_1, n = 51, 0.6$ ha). We estimated their diversity using an additive approach with three indices (richness, Shannon-Weiner, Simpson). Diversity was higher than expected at the "between aridity range ($\beta_3$)" scale, but lower at the "within-habitat scale ($\alpha_1$)". Alpha was higher than beta diversity for most spatial scales; and at the regional scale protected areas preserved a higher biodiversity than unprotected ones. Our results are the first to partition the diversity of desert small mammals at multiple spatial scales and to support the hypotheses of an irregular scale dependence of alpha and beta diversity when increasing the spatial scales. They also highlight that a better understanding of biodiversity patterns is gained when several tools are integrated and combined at different spatial scales.

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## 1. Introduction

Over the last three decades, conservation biologists and land managers have been seeking different strategies for biodiversity conservation. The most commonly used are keystone and umbrella species (Simberloff, 1998), rare or vulnerable species (Lawler et al., 2003), endangered habitats and particular processes. Ecological models such as population viability (Morris and Doak, 2002), niche theory (Chase and Leibold, 2003), species-area (Rosenzweig, 1995) or species-energy (Evans et al., 2005) relationships have also been essential when making management decisions. Nevertheless, these models and strategies are not totally efficient because of the absence (or weakness) of a broader framework able to include regional biodiversity patterns, the community level and the multiple-scale approach (Wagner et al., 2000; Gering et al., 2003) in the same analysis.

The relationship between spatial scale and diversity patterns, by comparing local and regional diversity or patch and local diversity, is currently a highly debated topic in ecology and macroecology (Caley and Schluter, 1997; Srivastava, 1999; Crist et al., 2003;

Rahbek, 2005). This model enables biologists to partition biodiversity into at least three components (Whittaker, 1972): alpha ($\alpha$, within-community diversity), beta ($\beta$, species replacement along environmental gradients or between-habitat diversity), and gamma ($\gamma$, regional species diversity in a range of habitats at landscape scale). Three main alternative hypotheses have been addressed about how alpha and beta change across spatial scales (Gering and Crist, 2002). The first is scale independence, which could be possible if alpha and beta remain stable or constant across gamma. The second hypothesis is constant scale dependence and is expected if alpha and beta grow constantly across the regional scale, while irregular scale dependence could occur if there are sudden transition zones across the regional scale (Gering and Crist, 2002). Different processes are able to explain each of the three above mentioned hypotheses.

This inter dependence between biodiversity and spatial scale could also change depending on the diversity measures used. For example, species richness is commonly used at regional or global scale, while species abundance and diversity are used at the local scale (measured as Shannon-Weiner index). It depends on the possibility of getting the accurate information for each spatial scale (richness is easier to measure at the regional scale, whereas abundance and diversity measures are easily obtained at the local scale). When dealing with multiple spatial scales there are several

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opinions on which index is more accurate. Lande (1996) recommended using similarity measures (such as evenness) within and among communities; whereas Jost (2006) preferred to use Shannon's entropy measure. The inclusion of several measures such as evenness, diversity and richness at the same spatial scale and across different spatial scales could improve understanding of diversity processes by including each index in a comparative way.

In desert biomes, small mammal biodiversity had been reported at different spatial scales. When considering the habitat-patch scale (0.16–1 ha), there are about three species (Kelt et al., 1996; Tabeni and Ojeda, 2005), while at the biome scale (more than 100,000 km$^2$), mammal richness is the highest in South American drylands because of the large number of endemic species (Mares, 1992). Despite the wide range of spatial scales at which small mammal diversity has been analyzed (Brown and Kurzius, 1987; Kelt et al., 1996; Shenbrot et al., 1999; Ojeda et al., 2000; Corbalán and Ojeda, 2004; Tabeni and Ojeda, 2005; Haythornthwaite and Dickman, 2006), studies relating diversity at more than two different scales are very scarce. Some studies focus on relationships between habitat patch and landscape scales, while others focus on regional to continental scales. To our knowledge there are no studies on partitioning of diversity of desert small mammals (either multiplicatively or additively) across a more inclusive range of scales.

In Argentina, the Monte Desert (hot desert) and Puna (high cold desert) are the biomes with the highest endemism and species richness of mammals (Ojeda et al., 2002). Despite the importance of this at a global scale, small mammals in the Monte Desert have only been studied from microhabitat (0.16–1 ha) to local scales (50 km$^2$), including habitat patchiness and species relationship with habitat features. Opposite results have been reported at the local scale, with either positive results for small mammal-heterogeneity patterns in different habitats within a protected area (Corbalán and Ojeda, 2004; Gonnet and Ojeda, 1998) or negative results (for some species) between protected and unprotected surrounding areas (Tabeni and Ojeda, 2005).

The objectives of our study were to characterize and quantify the patterns of diversity of small mammal assemblages in the Monte Desert at different spatial scales and under different land uses (protected versus unprotected areas). Specific questions addressed were: 1) How does small mammal diversity vary among habitat types?, 2) How is small mammal diversity partitioned additively into alpha, beta and gamma diversities across a spatial gradient?, 3) What is the functional form relating alpha and beta to gamma diversity when changing the spatial scale?, 4) How could the use of different diversity measures, indices or graphs influence decisions of wildlife managers?, and 5) Are protected areas efficient in protecting small mammal diversity at multiple spatial scales?

## 2. Materials and methods

### 2.1. Study area

Our study was conducted along a latitudinal range of 5° in Mendoza Province, Argentina (from 32° to 37°). This area belongs to the central portion of the Monte Desert biome (Morello, 1958). 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. Six habitat types were present in the study area: *Prosopis* woodland, *Larrea* shrubland, shrubland (other than *Larrea*), sand dunes, salt flat and pampas grassland (Morello, 1958) (Fig. 1).

### 2.2. Scale levels

Sample extent (geographical space where comparisons are made) was the landscape represented by the central portion of the Monte biome. Sample focus (area of inference) changed with scale, and sample grain (size of sample unit) remained constant throughout the scaling of diversity, with the lowest unit of analysis being within-habitat diversity.

Diversity was quantified at the regional biome scale and also partitioned into three levels of scaling. Regional diversity is the central part of the Monte Desert, considered as the upper level or gamma diversity (96,000 km$^2$) (Fig. 2). It was partitioned into six divisions along an aridity gradient (precipitation gradient) ($\alpha_3$, $n = 6$, 16,000 km$^2$). In each aridity division from two to four localities were selected, with within-localities being the $\alpha_2$ level ($n = 18$). Each locality included a total area of 2–3 ha and was separated from others by at least 60 km. Within each locality from two to four different habitat patches were selected ($\alpha_1$, $n = 51$), depending on habitat availability. Habitat patches were located 2–15 km apart and comprised 0.6 ha each. The lowest level included 6 band transects (4x250m = 0.1 ha) at least 500 m apart ($n = 306$) (Figs. 1 and 2).

A precipitation map published by the NAP (National Action Plan to Combat Desertification; 2003) was used in order to draw the aridity gradient of the central Monte Desert. Six precipitation belts, ranging from: 50–150, 150–250, 250–300, 300–350, 350–400 and 400–450 mm, were selected. The number of localities inside each precipitation range was selected depending on the total area occupied by each range. For example, the 300–350 mm range is the one with the largest area on the study site and therefore it had the highest number of sampled localities ($n = 4$); on the other hand, the 400–450 mm range includes the smallest area, with two localities surveyed. The remaining precipitation ranges included three sampled localities each. Each locality was considered a statistical replicate inside each aridity range for analyzing the scaling of biodiversity. Each locality was divided into different habitat types depending on their structural characteristics, following the classification proposed by Morello (1958). On each habitat type six statistically independent sampling sites were selected, as replicates of the habitat types in each locality.

This sampling design allowed us to consider $\alpha$ diversity without including environmental variability within patch diversity, which is considered to be an important issue when analyzing species diversity. If large areas were considered at the within-locality (or $\alpha$) diversity level, habitat heterogeneity could be included in the results of diversity. In this case, habitat heterogeneity could allow a fictitious co-occurrence of species that do not actually interact (Huston, 1999). This means that the first level of $\beta$ diversity is considered as falling within $\alpha$ diversity. In our study, by choosing an appropriate area size for small mammal sampling (0.6 ha), we ensured that habitat heterogeneity was really considered to be at $\beta_1$ sampling level (between habitats).

### 2.3. Habitat characterization

We quantified vegetation and structural variables using the modified point quadrant method (Passera et al., 1983), with 100 sampling stations along a 30-m long transect. One transect was placed inside each band transect, the lowest level of diversity, resulting in a total of 306 vegetation samples. Seven vegetation variables were quantified: tree cover, shrub cover, sub-shrub cover, grass cover, herb cover, bare soil and litter cover. A Kruskal–Wallis test for each vegetation variable was performed to assess the main features of the habitat. Plant cover was also used to estimate habitat heterogeneity, defined as the horizontal variation in habitat physiognomy (August, 1983). The Shannon-Weiner index (measured
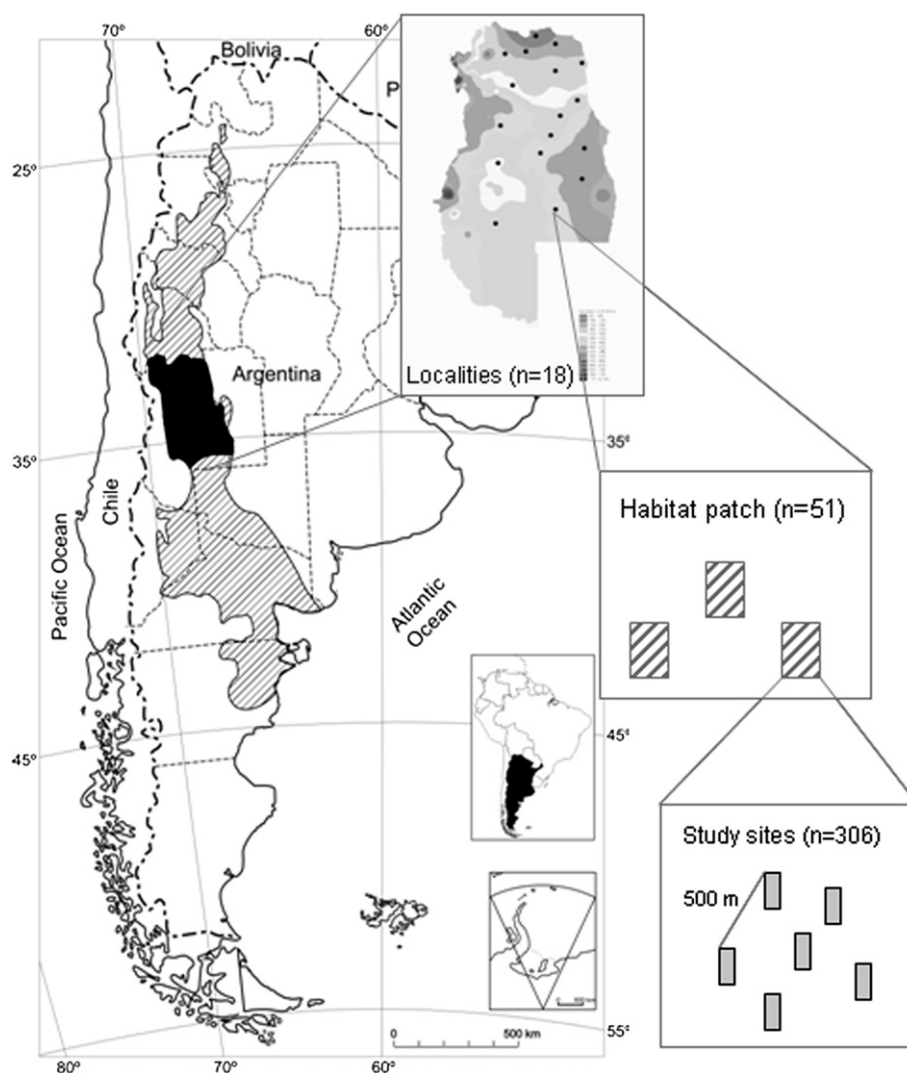
**Fig. 1.** Map of the study area and spatial design.

using the Ln scale) was used to estimate heterogeneity for each habitat type, and performed an ANOVA test to compare heterogeneity among habitats.

### 2.4. Small mammals sampling

Trapping was performed between September 2005 and June 2008 and sampling effort consisted of 23,000 night/traps. Our sampling efforts 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). In order to include and control temporal variability and improve the sampling design, we also sampled in the other seasons on randomly scattered sampling localities between aridity ranges. Detailed sampling dates are in Electronic Appendix 1. Small mammal sampling was conducted with live capture Sherman traps. Traps ($n = 25$; 10 m apart) were placed along a line transect on each band transect, and kept the system 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.

### 2.5. Regional community patterns

To describe community patterns in detail rank-abundance curves or "importance value curves" (Whittaker, 1972) were used. Small mammal assemblages between habitat types were compared by plotting one importance-value curve for each habitat type. The summarized $Log_{10}$ abundance of each species was considered for a regional approach (for detailed data on patch scale see Electronic Appendix 1). Relative abundance data were based on the number of different individuals caught during the three nights (i.e., recaptures not counted). Small mammal evenness was estimated with Simpson index. The Shannon-Weiner index was also used as a measure of regional diversity.

### 2.6. Additive partitioning of diversity

Gamma diversity was partitioned into the sum of the averages of diversity within samples ($\alpha$) and among samples ($\beta$)($\gamma = \beta + \alpha$). To extend it across multiple scales the additive equation proposed by Crist et al. (2003) was used. The additive model was preferred to the multiplicative one because it allowed us to include several spatial scales and analyze biodiversity using a single measure unit (Lande, 1996; Gaston et al., 2007). Alpha diversity at a given scale level is
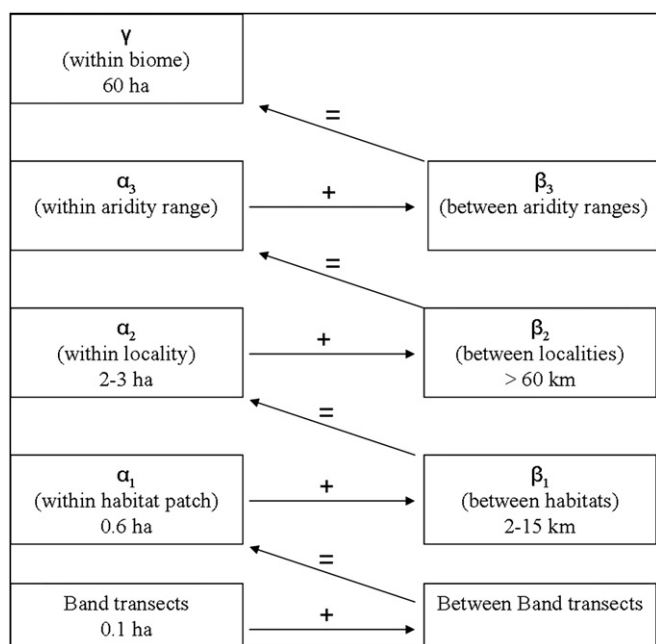
**Fig. 2.** Relationship between hierarchical levels in our additive partitioning model (read it from bottom to top). Diversity and scale extent are shown for each level.

the sum of alpha and beta diversity averages at the next lowest level, so overall gamma diversity can be described as:

$$\gamma = \alpha_1 + \sum \beta_i$$

where $i = 1$ is the lowest level of sampling and $i = m$ the highest one. In this study $\alpha_1$ is within-habitat diversity and $\sum \beta_i = \beta_1$ (between habitats) + $\beta_2$ (between localities) + $\beta_3$ (between aridity ranges). Beta diversity was calculated from the Shannon-Weiner index according to Lande (1996) as follows: $H'\beta = -\sum p_i \ln p_i - \sum q_j H'_j$, where $p_i$ is the proportional abundance of each species overall samples at this scale, and $q_j$ is an importance value of a sample of the total community. In our study, importance value refers to the number of habitat types available in each locality ($\beta_1$; expressed as a relative frequency), and to a proportional value of the total number of habitat types analyzed in the whole biome ($\beta_3$).

The PARTITION program (Veech and Crist, 2007) was used to calculate diversity across the whole region. Seven habitat patches were eliminated from this analysis because they recorded no captures (see Electronic Appendix 1 for details). To evaluate additive partitioning, we calculated observed values of $\alpha$, $\beta$ and $\gamma$ based on species richness, Shannon-Weiner and Simpson indices (Lande, 1996). Observed and expected values for $\alpha$ and $\beta$ diversity were compared by running the program with 1000 iterations (boot-strapping) and testing the statistical significance of the observed values. Randomization was run for all three $\alpha$ levels with both non-balanced and individual-based samples.

### 2.7. Protected vs. unprotected areas

Small mammal diversity between protected and unprotected areas was compared to determine how well the regional protection system (in the central Monte Desert) protects small mammal diversity at a regional scale. Each sampled locality ($n = 18$) was classified as protected ($n = 7$) or unprotected area ($n = 11$). Protected areas included all state parks, private parks and RAMSAR sites present in the Monte Desert region of the Mendoza Province. Unprotected areas include private or government public lands.

A rarefaction analysis was used to compare species richness between protected and unprotected areas. An individual-based rarefaction curve was preferred over sample-based rarefaction curves (Gotelli and Colwell, 2001). This individual rescaling allowed us to compute the number of individuals for each sampling level, instead of taking the mean for number of individuals (Gotelli and Colwell, 2001). The curves were based on 500 randomizations without replacement, and constructed with the use of the EstimateS program (Colwell, 2006). An ANOVA test was performed to test for statistical differences between small mammal diversities between protected and unprotected areas.

## 3. Results

### 3.1. Habitat characterization

Habitat characteristics, defined by structural components (variables), are shown in Table 1. Bare soil was higher in sand dunes and salt flat, whereas litter cover dominated the *Prosopis* woodland and pampas grassland. The *Prosopis* woodland was the only habitat with tree cover. Shrubs were dominant in the *Larrea* shrubland, and sub-shrubs in the *Prosopis* woodland and salt flat. Sand dunes were characterized by herbs and grasses, and the pampas grassland by perennial grasses (*Cortadeira* sp.).

In terms of habitat heterogeneity, habitat types were significantly different ($F = 9.34$; $p < 0.0001$). The most complex type was *Prosopis* woodland ($H = 1.62$), followed by shrubland ($H = 1.55$) and sand dunes ($H = 1.54$). Salt flat ($H = 1.43$) and *Larrea* shrubland ($H = 1.36$) were next in heterogeneity, but they have high levels of standard deviation. The Pampas grassland was the habitat with the lowest heterogeneity ($H = 0.92$).

### 3.2. Regional small mammal community patterns

A total of 411 individuals from 12 species were captured during this study, with a capture success of 2.6%. Three Rodentia families were present: 1) Cricetidae: *Eligmodontia typus*, *Eligmodontia moreni*, *Graomys griseoflavus*, *Thylamys pallidior*, *Calomys musculinus*, *Phyllotis xanthopygus*, *Akodon molinae*, *Akodon* sp., *Abrothrix andinus*, *Salinomys delicatus* and, 2) Caviidae: *Microcavia australis*, and 3) Octodontidae: *Tympanoctomys barrerae*. These species account for 65% of the Monte Desert small mammal richness found by Ojeda and Tabeni (2009).

At the patch scale, species richness per habitat type varied from one to five, with the mean being two (Electronic Appendix 1). At regional scale, the richest habitat was the shrubland with nine species, followed by *Prosopis* woodland and sand dunes (seven species; Fig. 3). The poorest habitat was the salt flat with four species. Simpson index for estimating evenness structure showed similar values for five habitat types (ranging from 0.39 to 0.43)

**Table 1**
Medians, statistical value (H′) and *p* values for Kruskal−Wallis are reported for each habitat variable. Reported data are presented in percent values. PW = *Prosopis* woodland; SD = Sand dunes; LS = *Larrea* shrubland; SF = Salt flat; Sh = shrubland; PG = Pampas grassland.

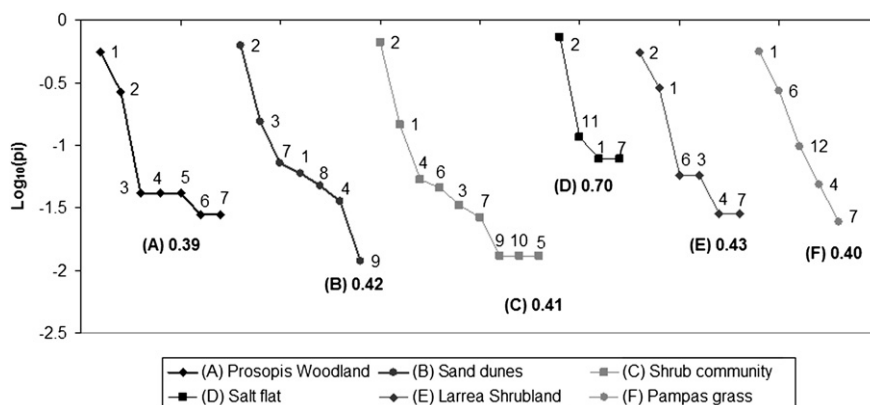|  | PW | SD | LS | SB | Sh | PG | H′ | p |
|---|---|---|---|---|---|---|---|---|
| Bare soil | 17 | 28 | 21.5 | 41.5 | 33.5 | 3 | 44.85 | <0.0001 |
| Litter | 76.5 | 66 | 71.5 | 47.5 | 56 | S4 | 32.15 | <0.0001 |
| Herbs and Grasses | 24.5 | 47.5 | 12.5 | 7 | 11 | 11 | 38.21 | <0.0001 |
| Sub-shrubs | 27 | 17 | 11.5 | 29.5 | 16.5 | 0 | 29.3 | <0.0001 |
| Shrubs | 85.5 | 49.5 | 121 | 26.5 | 68 | 0 | 87.18 | <0.0001 |
| Trees | 46.5 | 0 | 0 | 0 | 0 | 0 | 74.23 | <0.0001 |
| Perennial grasses | 0 | 0 | 0 | 0 | 0 | 256 | 46.5 | <0.0001 |

**Fig. 3.** Rank-abundance curves for six habitat types. 1-*Graomys griseoflavus*; 2-*Eligmodontia typus*; 3-*Eligmodontia moreni*; 4-*Thylamys pallidior*; 5-*Salinomys delicatus*; 6-*Akodon molinae*; 7-*Calomys musculinus*; 8-*Abrotrix andinus*; 9-*Microcavia australis*; 10-*Phyllotis xanthopygus*; 11-*Tympanoctomys barrerae*; 12-*Akodon sp.* Evenness values obtained from Simpson index appear in bold.

with the exception of the salt flat, which had the lowest evenness (0.70). Even though the Shannon-Weiner index showed no significant differences between small mammals per habitat type, there was a tendency of decreasing biodiversity depending on the habitat type (*Prosopis* woodland = 0.64; Pampas grassland = 0.57; Shrubland = 0.53; San dune = 0.52; *Larrea* shrubland = 0.44; Salt flat = 0.21).

*Phyllotis xanthopygus* was restricted exclusively to the shrubland, whereas *T. barrerae* was typical of the salt flat. *G. griseoflavus* was dominant in the *Prosopis* woodland and pampas grassland, whereas *E. typus* abundance was higher in sand dunes, *Larrea* shrubland, salt flat and shrubland. *C. musculinus* was present in the *Prosopis* woodland, salt flat, shrubland and *Larrea* shrubland, although it was the species with the lowest abundance in all of them. The genus *Eligmodontia* was one of the dominant species in all habitats, except for the pampas grassland where it was absent.

### 3.3. Additive partitioning of diversity

Alpha diversity ($\alpha_1$) was lower than expected from randomization for all three indices (Table 2). Observed values of between-habitat diversity ($\beta_1$) were significantly lower than expected only for species richness. Between-locality diversity ($\beta_2$) also showed statistical differences between expected and observed values, with observed values being higher than expected for either Shannon-Weiner or Simpson index, but lower for species richness (Table 2). In between-aridity divisions ($\beta_3$), observed values were higher than expected by chance for all indices.

By analyzing the individual contribution of each diversity measure to each index (Table 2), the highest species richness was observed for between-aridity divisions ($\beta_3$), with more than 50% of the total species richness. For the Shannon-Weiner index, within-habitat diversity ($\alpha_1$) contributed around 40% of gamma diversity,

whereas $\beta_2$ and $\beta_3$ accounted for around 20% each. The contribution of within-habitat diversity ($\alpha_1$) to regional biodiversity was more than 80% for the Simpson index (Table 2). At all diversity indices, between-habitat diversity ($\beta_1$) was the lowest contributor to the gamma diversity of small mammals.

By comparing beta and alpha diversities along the sampling scales (Table 2; Fig. 4), different results were found depending on the index used. For species richness, a gradual increase in both alpha and beta diversities were found. At habitat and locality levels, alpha was higher than beta; whereas at the aridity division scale, beta diversity was slightly higher than alpha. Using the Shannon-Weiner index, a similar pattern of parallel increase in alpha and beta diversities with increasing the scale was found. Nevertheless, differences between alpha and beta diversities were more pronounced as the scale increased from patch to regional level. Using the Simpson index, a marked dominance of alpha diversity at all sampling levels was found, with beta diversity being totally insignificant. As a general pattern, alpha diversity was higher than beta diversity at most spatial scales, independently of the index used.

### 3.4. Protected vs. unprotected areas

All protected areas in the central part of Monte Desert are between 50 and 350 mm precipitation ranges: 50–150 (Huanacache and Telteca), 150–250 (Villavicencio), 250–300 (Nihuil), 300–350 (Divisadero, Ñacuñán and Llancanelo) (Electronic Appendix 1). There are no protected areas for the sampled 350–450 range or higher.

Rarefaction curves between both large divisions showed that species richness can be compared for approximately 172 sampled individuals, with 7.6 species for unprotected areas and 10 for protected ones (Fig. 5). Nevertheless, this difference was not statistically significant for the Shannon-Weiner diversity index ($p = 0.98$).

**Table 2**
Observed and expected values for different diversity measures.

| Scale level | Diversity measure | Species Richness | | | | Shannon Diversity | | | | Simpson Diversity | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | # | OBS. | EXP. | *p* | H' | OBS. | EXP. | *p* | S | OBS. | EXP. | *p* |
| Patch | α1 (within habitats) | 2.2 | 18.33 | 28.33 | **<0.0001** | 0.585 | 39 | 61.4 | **<0.0001** | 0.538 | 80.9 | 102.94 | **<0.0001** |
| | β1 (between habitats) | 1.1 | 9.17 | 15 | **<0.0001** | 0.231 | 15.44 | 16.4 | =0.296 | 0.0137 | −2.06 | −2.1 | =0.516 |
| Local | α2 (within localities) | 3.3 | 27.5 | 43.33 | **<0.0001** | 0.816 | 54.44 | 77.8 | **<0.0001** | 0.5249 | 78.84 | 100.84 | **<0.0001** |
| | β2 (between localities) | 2.5 | 20.83 | 25 | =0.03 | 0.319 | 21.28 | 14.53 | **<0.0001** | 0.0607 | 9.12 | −0.58 | **<0.0001** |
| Aridity range | α3 (within aridity division) | 5.8 | 48.33 | 68.33 | **<0.0001** | 1.135 | 75.72 | 92.33 | **<0.0001** | 0.5856 | 87.96 | 100.26 | **<0.0001** |
| | β3 (between divisions) | 6.2 | 51.67 | 32.5 | **<0.0001** | 0.364 | 24.28 | 7.6 | **<0.0001** | 0.0819 | 12.3 | −0.02 | **<0.0001** |
| Regional | γ (within Central Monte Desert) | 12 | 100 | 100.83 | | 1.499 | 100 | 99.93 | | 0.6675 | 100.26 | 100.24 | |

Significant values (*p*) are indicated in bold.

## Species Richness



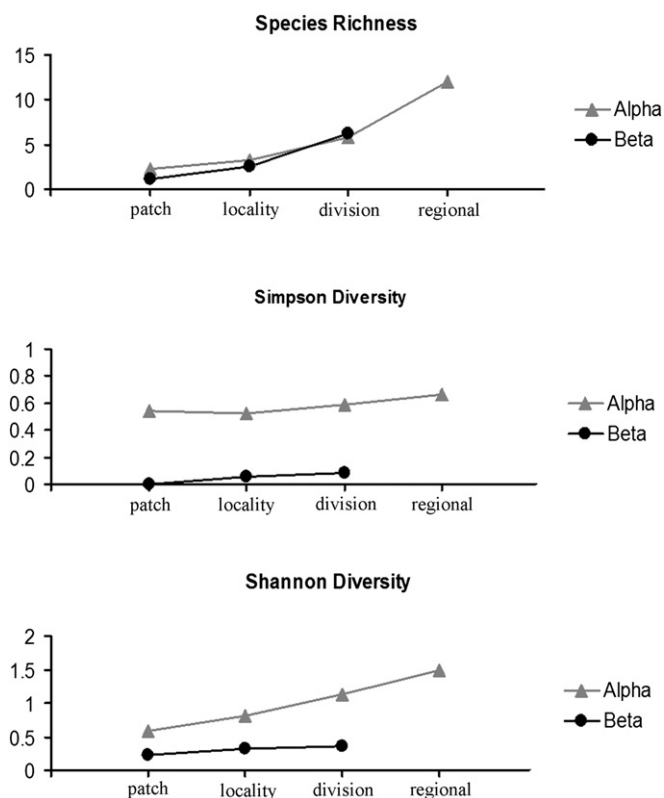## Simpson Diversity



## Shannon Diversity



**Fig. 4.** Trends in alpha and beta diversities with increasing sampling levels (within and between scales).

## 4. Discussion and conclusions

This study is the first to partition the diversity of desert small mammal assemblages at multiple spatial scales and with multiple diversity measures. Our results suggest that alpha and beta diversities are both necessary when analyzing biodiversity patterns across a scale gradient because the relative importance of each one changes with scale. The diversity pattern at the regional scale is mainly explained by species turnover (beta diversity) while at the local scale, within patch diversity is the main factor driving the observed pattern. Our findings support the hypothesis of irregular dependence of alpha and beta diversity across the spatial scale proposed by Gering and Crist (2002). Even though we did not directly deal with the processes that govern these observed patterns, we suggest that the main factor influencing regional species turnover (beta diversity) is the precipitation gradient.
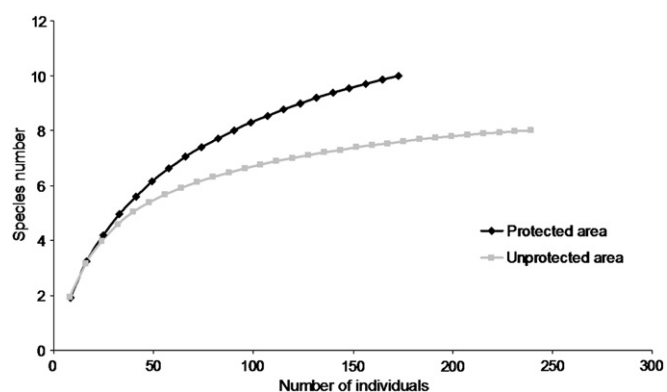


**Fig. 5.** Individual-based rarefaction curves for protected and unprotected areas in the Monte Desert.

### 4.1. Question 1: How does small mammal diversity vary between habitat types?

At the regional scale we found no statistical differences in small mammals' diversity across habitat types. Even so, when considering species identity there is a clear evenness and distinctiveness of desert assemblages with rare species such as *T. barrerae* and *S. delicatus*, which only occur in salt flats and have specific behavioural, morphological and physiological adaptations to that type of habitat (Diaz and Ojeda, 1999; Giannoni et al., 2000; Lanzone et al., 2005). These attributes of distinctiveness and evenness of the Monte Desert highlights the priority of conservation of desert ecosystems (Mares, 1992; Ojeda et al., 2000). Although there was no clear differentiation among small mammal assemblages between habitat types at the regional scale, rodent species of desert systems do select habitat at the micro and macro habitat scales (Gonnet and Ojeda, 1998; Corbalán and Ojeda, 2004; Tabeni and Ojeda, 2005; Stevens and Tello, 2009). Therefore, when analyzing diversity patterns, habitat use should be considered at a wide range of spatial scales in order to understand how the species are assembled.

### 4.2. Question 2: How is small mammal diversity partitioned additively into alpha, beta and gamma diversities across a spatial gradient?

We found an increase of alpha diversity when increasing the spatial scale. Different processes can drive the observed patterns of how biodiversity can change with scale (Chandy et al., 2006). A low $\alpha$ diversity is expected at the patch scale if inter or intra specific interactions are stronger and dominate the regulatory processes of the observed pattern (Loreau, 2000). Conversely, at larger spatial scales (i.e. regional) interspecific interactions are weaker or undetectable, and other factors such as climate, topography or soil characteristics are the ones regulating the observed pattern (Huston, 1999; Loreau, 2000). In our study, the high $\alpha$ diversity at the regional scale was related to the precipitation pattern, while at the patch scale habitat structure did not support the biodiversity pattern. We suggest analyzing other local factors such as interspecific interactions (i.e. trophic niche segregation) as potential causes of the observed structure of small mammal assemblages at the smaller spatial scales.

Species richness also showed high beta diversity at the "aridity range" scale. This pattern indicates that the turnover of species along the aridity gradient of the Monte Desert is more important for structuring regional biodiversity than biodiversity within each aridity range. The low values of $\beta$ diversity on the lowest spatial scales (locality and patch levels) implies that small mammal diversity is not different enough among those levels of analysis. These results are consistent with the first hypothesis proposed by Legendre et al. (2005) about the origin of $\beta$ diversity which states that "species composition is uniform over large areas". In other words, when species turnover is small at the local or patch scale, assemblages are mainly dominated by a limited number of species and regulated by biological interactions such as competition or facilitation (Pitman et al., 1999). Pitman's assertion is supported by the presence of two generalist rodents, in terms of diet and habitat, as the dominant species of Monte Desert small mammal assemblages (*E. typus* and *G. griseoflavus*) (Giannoni et al., 2005; Corbalán, 2006).

### 4.3. Question 3: What is the functional form relating alpha and beta to gamma diversity when changing the spatial scale?

Gering and Crist (2002) proposed three alternative and mutually exclusive hypotheses that answer this question: a) scale independence, b) regular dependence, and c) irregular independence. Our

results show low values of alpha and beta diversity at the patch scale ($\alpha = 18.33$; $\beta = 9.17$) and high values at the regional scale ($\alpha = 48.33$; $\beta = 51.67$), with a non uniform exchange of diversities as the scale increases. These results support the hypothesis of irregular dependence of biodiversity because alpha and beta's contributions to regional biodiversity show a significant and non linear change along a gradient of spatial scales. Similar patterns were reported previously on insect communities (Gering and Crist, 2002). This irregular dependence of alpha and beta to gamma diversity implies that the ecological processes that drive community structure are different at each spatial scale. Processes that can act mainly at the patch scale are stress tolerance, limitations to abiotic factors, anti- predator strategies and competitive abilities, among others (Kneitel and Chase, 2004). At the local scale, including habitat heterogeneity, the most important processes could be the degree of specialization or habitat generalization, patch colonization (source-sink) and competitive ability (Kneitel and Chase, 2004). At the regional scale, processes are related to regional or biogeographic factors such as precipitation or temperature gradients, topography and soil characteristics, as well as the biogeographical history of each species (Willig et al., 2003).

### 4.4. Question 4: Are protected areas efficient in protecting small mammal diversity at multiple spatial scales?

There where no differences on small mammal diversity between protected and unprotected areas. Nevertheless, if we project rarefaction curves of species numbers for protected and unprotected areas, we can expect that protected ones will have an increase in their diversity whereas unprotected ones will remain stable at about eight species. Despite that the species exchange between aridity ranges is the most relevant factor at the regional scale, there is a lack of protected areas in the precipitation belt ranging between 350 and 550 mm. The rare and endemic species *T. barrerae* and *S. delicatus* were mainly present in protected areas, particularly on RAMSAR sites (Llancanelo and Huanacache), but also in an unprotected area ("El Tapón") northeast of Mendoza Province.

Previous reports comparing mammal biodiversity between protected and unprotected areas in the Monte Desert showed that grazing affects small mammals community structure and that population abundance depends on the habitat heterogeneity (Gonnet and Ojeda, 1998; Tabeni and Ojeda, 2005; Tabeni et al., 2007). In the protected areas of the Monte Desert, human activities such as cattle grazing and logging, are not allowed. These restrictions result in complex and heterogeneous "islands" surrounded by a disturbed matrix. Species that occupied open habitats (i.e., *E. typus, D.patagonum*) were favored by grazing activities (Corbalán et al., 2006; Rodríguez, 2009); meanwhile species adapted to more complex habitats (i.e., *G. griseoflavus, A. molinae, C. musculinus*) preferred protected areas (Tabeni and Ojeda, 2005; Corbalán et al., 2006; Tabeni et al., 2007). Although the direct effect of these factors on small mammal communities has not been proven, they should be taken into account when analyzing biodiversity not only at a local but also a regional scale.

### 4.5. Question 5: How could the use of different diversity measures, indices or graphs influence decisions of wildlife managers?

On a first view, our results indicate different recommendations for conservation purposes, depending on the indices used. If we analyze species richness alone, the interchange of species between places with different aridity range ($\beta_3$) should be the focal scale for conservation actions. However, if we focus on diversity measures (Simpson or Shannon-Weiner indices), then $\alpha$ diversity at the patch scale will be the highest contributor to regional biodiversity. When integrating diversity indices, species richness and rank-abundance curves, we found that the maximum species diversity and evenness occurred at the patch scale.

As the Shannon-Weiner index is significantly lower than the Simpson index, the most common species are not evenly distributed at the patch scale (Gering et al., 2003). This interdependence of patterns of variance in biodiversity components ($\alpha$ and $\beta$) with different diversity measures (indices) was also recorded for other groups like plants and invertebrates (Wagner et al., 2000; Crist et al., 2003; Gering et al., 2003; Stendera and Johnson, 2005; Chandy et al., 2006).

Despite recommendations to focus on particular indices (Lande, 1996), or to not focus on some (Jost, 2006), we suggest a combined and integrated use of different biodiversity tools when analyzing biodiversity at different spatial scales. Inappropriate management recommendations could be issued when focusing on a single measure of biodiversity. Additive partitioning of species diversity is a powerful tool in conservation biology because of its inclusive theoretical and methodological framework. It can be applied when comparing biodiversity between regional and local scales or between protected and unprotected areas (Crist et al., 2003; Gering et al., 2003), among others.

The collective understanding of species richness, Shannon-Weiner and Simpson indices, and Rank-abundance curves, offer a deeper understanding of assemblage structure at different spatial scales. Appropriate implementation and interpretation of these results are directly related to a more thorough knowledge of the natural history of the system studied, particularly when identifying appropriate factors driving biodiversity at the regional scale.

### Appendix. Supplemental material

Supplementary data related to this article can be found online at doi:10.1016/j.jaridenv.2010.12.007

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