

Original article

Scaling the relative dominance of exogenous drivers in structuring desert small mammal assemblages



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ARTICLE INFO

Article history:

Received 11 August 2015
 Received in revised form
 30 September 2015
 Accepted 22 October 2015
 Available online xxx

Keywords:

Small mammals
 Community structure
 Arid lands
 Exogenous drivers
 Spatial scales

ABSTRACT

Assemblage patterns could be primarily generated by two types of drivers: exogenous (such as environmental and climatic factors) and endogenous (interactions such as competition, predation, mutualism or herbivory). The most widely accepted hypothesis states that at smaller scales (such as patch scale), interspecific interactions are the major drivers structuring communities, whereas at larger regional scales, factors such as climate, topography and soil act as ecological filters that determine assemblage composition. The general aim of this paper is to compare different exogenous drivers in terms of their relative dominance in structuring desert small mammal communities across a range of spatial scales, from patch to regional, and compare them with previous results on endogenous drivers. Our results show that as spatial scale increases, the explanatory power of exogenous factors also increases, e.g. from 17% at the patch scale (i.e. abundance) to 99% at the regional scale (i.e. diversity). Moreover, environmental drivers vary in type and strength depending on the community estimator across several spatial scales. On the other hand, endogenous drivers such as interspecific interactions are more important at the patch scale, diminishing in importance towards the regional scale. Therefore, the relative importance of exogenous versus endogenous drivers affects small mammal assemblage structure at different spatial scales. Our results fill up a knowledge gap concerning ecological drivers of assemblage structure at intermediate spatial scales for Monte desert small mammals, and highlight the importance of dealing with multi-causal factors in explaining ecological patterns of assemblages.

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1. Introduction

Understanding the processes that shape assemblage structure is one of the central themes in community ecology (Shenbrot et al., 1999). Two major theoretical sets of hypotheses are recognized. On the one hand, exogenous drivers (such as environmental and climatic factors) are considered to be the main drivers of species diversity, exerting a bottom–up effect through the system (Porter et al., 2000; Ruggiero and Kitzberger, 2004). Alternatively, interspecific interactions (such as competition, predation, mutualism or herbivory) may shape species diversity through a top–down effect, acting as endogenous drivers (Shenbrot et al., 1999; Kelt, 2011). The relative importance of one or the other driver could vary depending on the spatial or temporal scale (Willis and Whittaker, 2002; Storch et al., 2007). Although scaling of assemblage patterns has often

been addressed in the literature (Kelt, 2011; Rodríguez and Ojeda, 2011, 2013), scaling of assemblage processes is a less common topic. The most widely accepted hypothesis states that at smaller scales (such as the local patch scale), interspecific interactions are the major driver structuring communities, whereas at higher regional scales, factors such as climate, topography and soil act as ecological filters that determine assemblage composition (Huston, 1999; Willis and Whittaker, 2002).

With the current interest in climate change, exogenous drivers have been frequently examined for estimating the potential risk of local extinction of vulnerable species (Fleishman, 2010). Some authors even argue that it is only necessary to understand how species respond to climate, independently of controlling endogenous factors, to be able to understand the way populations auto regulate themselves as well as the dynamics of the community, particularly in arid systems (Noy-Meir, 1979).

In most arid systems, precipitation is an irregular, unpredictable and usually scarce resource, and one of the major drivers structuring mammal assemblage patterns through its effect on limiting

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plant growth and primary production (Abramsky and Rosenzweig, 1984; Whitford, 2002). In these cases, there is a bottom–up effect from precipitation to predators throughout the food chain (Letnic et al., 2005), which can act via two different mechanisms. Precipitation can directly affect survival and reproduction rates of some species, or indirectly regulate food availability by limiting primary production (Lima et al., 2006). Another of the most important exogenous factors that could structure assemblage patterns in desert systems is ambient temperature, mainly because arid lands are characterized by highly variable and extreme temperatures (daily and seasonally) (Whitford, 2002). For example, changes in the activity rhythms of some desert small mammals are associated with ambient temperature variation (Dickman et al., 2001). Habitat heterogeneity and habitat complexity are also exogenous drivers that could regulate the structure of desert assemblages by generating different macro and microhabitats that can be selected or avoided by some species (González-Megías et al., 2007; Albanese et al., 2011).

The interaction of exogenous factors with different descriptors of assemblage patterns could take different forms depending on the spatial scale or community descriptor used, which makes it difficult to establish a general pattern (González-Megías et al., 2007). Nevertheless, it is hypothesized that the strength of exogenous drivers increases with increasing spatial scale (Loreau, 2000), with evolutionary processes being more important at higher spatial scales and ecological ones at smaller scales, and therefore promoting a nested nature of drivers (Clarke, 2007).

Over the last 40 years, desert small mammals have been used as an ideal model in community ecology, mainly because their assemblages are simple but diverse, and species are conspicuous and abundant (Shenbrot et al., 1999). The structure of desert small mammal communities has been evaluated locally and regionally in a variety of deserts worldwide (Kelt, 2011), but only in the Monte Desert (South America) and Simpson Desert (Australia) has this analysis been done across several spatial scales (Rodríguez and Ojeda, 2011; Haythornthwaite and Dickman, 2006 respectively). Particularly in the Monte desert, the diversity of small mammals shows an irregular pattern across spatial scales (Rodríguez and Ojeda, 2011); this suggests that alpha and beta diversities contribute in a nonlinear way to regional diversity along a gradient of increasing spatial scales (Gering and Crist, 2002). These results, coupled with an increase in nested patterns on higher spatial scales (Rodríguez and Ojeda, 2013), indicate that the ecological processes driving community structure are different at each spatial scale. Thus, scaling the relative importance of different exogenous drivers could shed light on the underlying causes that promote this general community pattern.

The general aim of this paper is to compare different exogenous drivers in terms of their relative dominance in structuring desert small mammal communities across increasing spatial scales, from local patch to regional. In Monte desert small mammal assemblages, we expect a growing influence of exogenous drivers as spatial scales increases, since assemblages in this area show an irregular pattern. Moreover, we posit that different community estimators are explained by different exogenous drivers at different spatial scales; with the most common estimator (diversity index) not merely being the most proper one for all spatial scales.

2. Materials and methods

2.1. Study area, sampling design and small mammal trapping

This study was conducted in the Monte Desert biome (Argentina, South America). The climate is arid to semi-arid and markedly seasonal, with warm, rainy summers and cold, dry

winters. Average annual rainfall ranges from 50 mm to 450 mm and mean temperature from <10° C in winter to >20° C in summer. Habitat heterogeneity and patchiness are major features of the Monte Desert (Morello, 1958).

Small mammal assemblages were quantified along a 5° latitudinal range in Mendoza Province (from 32° to 37° south latitude) at three spatial scales: habitat patch, locality, and region (Fig. 1). Regional assemblages were quantified across the central part of the Monte Desert (96,000 km²) (Fig. 1). This area was partitioned into six precipitation ranges along an aridity gradient ($n = 6, 16,000 \text{ km}^2$ each). Two to four localities were selected in each aridity division, totaling 18. Each locality covered a total 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 within each locality. The boundaries between patches were ecological. 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 scale component for each spatial scale. We followed the terminology and concepts by Scheiner et al. (2000). Sample extent (geographical space where comparisons are made) was the landscape encompassed by the central portion of the Monte Desert biome and remained constant throughout all spatial scales. Sample grain (size of sample unit) and sample focus (area of inference) changed with scale, but remained the same within each scale as follows: 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 km².

Trapping was performed between September 2005 and June 2008 with total sampling effort being 23 000 trap/nights. Sampling effort was conducted mainly between January and June of each year because Monte Desert small mammals have their peak abundance during this period (Corbalán, 2004; Albanese, 2010). Moreover, we sampled some localities in other periods of the year to control temporal variability, with a random sampling design at the regional scale. Small mammal sampling was conducted with live-capture Sherman traps (Petit and Waudby, 2012). Twenty five traps were placed along a line transect (10 m apart) on each band transect, and the system was kept active during three consecutive nights using peanut butter and oat for bait. Captured animals were identified to species level, marked with picric acid for individual identification, and then released.

2.2. Community descriptors

We used five community descriptors (richness, abundance, diversity, evenness, and biomass) at each spatial scale. Species Richness (S') was estimated as the number of species recorded on each sampling unit. At the patch scale, it was estimated as the number of species per site, because each site had the same sampling effort (450 trap/nights). At the locality and regional scales, we estimated relative richness according to sampling effort, because the number of sampling units depends on habitat availability. We used the following equation,

$$S' = S / (\# \text{habitat patch} * 450 \text{trap/night}) * 100$$

where S is absolute richness and S' relative richness.

Diversity was estimated using the Shannon index (H') according to the following equation:

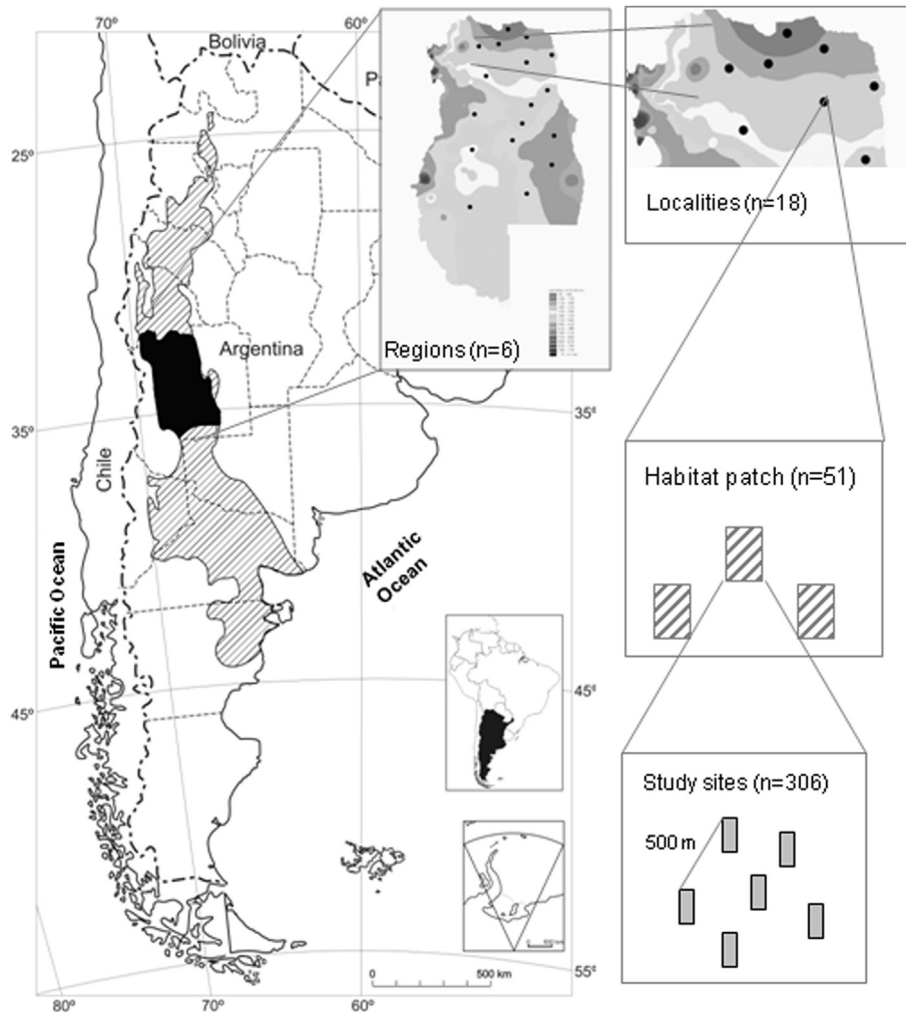


Fig. 1. Study area in the Monte desert (Argentina, South America) and sampling design. Dashed lines delimit the Monte desert biome, the black spot is the location of the central portion of the Monte desert where sampling was conducted. Shaded areas in region and locality panels indicate the precipitation gradient. The number of sampling units for each spatial scale is indicated in brackets.

$$H' = -\sum_{i=1}^S p_i \ln p_i$$

where S is number of species and p_i the relative abundance of each species (Magurran, 2004).

Evenness was estimated for each spatial scale using the Simpson index (D) according to the following equation:

$$D = \sum_{i=1}^S p_i^2$$

where p_i is the proportion of individuals of species i in an infinite community (Magurran, 2004).

Biomass (B) was estimated at each spatial scale using the equation:

$$B = \sum_{i=1}^S b_i \cdot n$$

where b_i is the average weight of species i and n the number of individuals of species i captured at each sampling site (patch, locality or region).

2.3. Environmental descriptors

We estimated three groups of variables for each spatial scale: habitat, topographic and climate variables. At the patch scale, habitat variables include habitat heterogeneity, habitat complexity and habitat type. Habitat heterogeneity is considered to be the horizontal variation in habitat physiognomy, whereas habitat complexity is the variation in vertical strata within a habitat (August, 1983). These variables were measured along each band transect ($n = 306$) by using the modified Point Quadrat method (Passera et al., 1983) on a 30-m long line transect with 100 sampling points 30 cm apart. At each sampling point we recorded the vertical distribution of plants by noting every species present at 25 cm intervals from ground level to 2 m high, which yielded nine vertical layers. Sixteen habitat variables were quantified: percent cover of bare soil, litter, grasses, forbs, sub-shrubs (<1 m h), shrubs, trees and nine vertical layers every 25 cm. Heterogeneity and complexity were quantified for each sampling site using the Shannon diversity index (Mac Arthur and Mac Arthur, 1961). The variable habitat type was included in the analyses as a factor: *Prosopis* woodland, *Larrea* shrubland, non-*Larrea* shrubland, sand dunes, salt flat and pampas grassland (Morello, 1958). At the locality scale, habitat type was not included because several habitat types occurred within each

locality, making classification problematic. Habitat heterogeneity and complexity were estimated as the mean value of all sampled patches at each locality. At the regional scale, habitat type was not considered either because of the multiple habitats present. Habitat complexity and heterogeneity were estimated as the mean value of all sites sampled within each precipitation range.

Topographic variables include soil hardness and altitude above sea level. Soil hardness was estimated using a 70-cm long penetrometer with a 500-g mace. Within a 30-cm radius of every trap location we estimated the variable “depth (in cm) at which the penetrometer penetrated with 2 mace punches”. Sampling effort varied according to scale: $n_{\text{patch}} = 150$, $n_{\text{locality}} = 300\text{--}600$, $n_{\text{region}} = 900\text{--}1800$. Altitude was estimated using a GPS device.

Climate variables utilized were mean annual precipitation and mean annual temperature. Both variables were obtained from the World Clim Data Base and verified with local weather stations: El Mateo, in Lavalle (32° 14' 31.00" S, 67° 41' 24.00" W, 512 m a.s.l.), Ñacuñán, in Santa Rosa (34° 02' 43.19" S, 67° 56' 6.49" W, 572 m a.s.l.) and Cochicó, in General Alvear (35° 43' 58.00" S, 67° 21' 03.00" W, 440 m a.s.l.). Both variables were estimated at all three spatial scales ($n_{\text{patch}} = 51$, $n_{\text{locality}} = 18$, $n_{\text{region}} = 6$) as the mean value of each sampling unit.

2.4. Data analysis

To evaluate which variables best explain each community descriptor at each spatial scale, we performed multiple regressions using Generalized Linear Models (GLM). First, we performed a distribution analysis of each variable at each spatial scale using distribution-fitting test. The selected link function for these analyses depends on the type of distribution of the response variables (McConway et al., 1999). Additionally, to avoid inclusion of redundant explanatory variables, we performed correlation analyses among the independent variables using partial Pearson correlation analysis. Only uncorrelated variables were included ($p > 0.05$).

Complete or full models for each dependent variable and for each spatial scale were compared with reduced or nested models using Akaike Information Criteria (AIC). To compare models, we also estimated ΔAIC by using the following equation: $\Delta\text{AIC}_i = \text{AIC}_i - \text{minAIC}$, where minAIC is the lowest value of all models (Burnham and Anderson, 2002). Two models were considered significantly different if $\Delta\text{AIC} > 2$ (Burnham and Anderson, 2002). We also estimated the percentage of explained deviance for each model and its p value. In significant models, we also estimated the percentage of explained deviance for each variable within the model. Because not all explanatory variables showed a linear relationship with the response variable, we also utilized quadratic regression models on each variable at each spatial scale and estimated 95% Confidence Intervals (CI). We used Genstat and Statistic software to perform GLM analyses (McConway et al., 1999).

3. Results

3.1. Patch scale

Abundance was better explained by mean annual precipitation, mean annual temperature and altitude (Table 1). All three variables were negatively associated with abundance and the entire model explained only 17.4% of the total variance (Table 1). Precipitation was the most explanatory variable (9.7% of explained deviance), followed by temperature (4.9% of explained deviance) and altitude (2.8% of explained deviance) (Table 1). Species richness was negatively explained by altitude (8.4% of explained deviance) (Table 1), whereas evenness, biomass and biodiversity were not related to any explanatory variable ($p > 0.11$).

Quadratic regressions showed that altitude explained 10.5% of species richness (8.46% linear and 2.02% quadratic) (Fig. 2-13; Supporting information). Small mammal abundance and biomass could not be explained by any quadratic function. Finally, biodiversity and evenness were associated with precipitation in a hump-shaped manner, explaining 10.9% and 12.4% respectively, indicating that the least diverse and least even sites lie within the intermediate precipitation range (Fig. 2-24–25; Supporting information).

3.2. Locality scale

Relative abundance was negatively associated with altitude (explained deviance: 42.1%), habitat complexity (explained deviance: 3.7%), mean annual precipitation (explained deviance: 1%) and mean annual temperature (explained deviance: 0.3%) (Table 1). Small mammal evenness was negatively associated with habitat complexity (explained deviance: 29.5%) and positively associated with mean annual temperature (explained deviance: 16.5%), explaining 46.1% of total deviance (Table 1). Therefore, the assemblages with higher species evenness were those present at the site with less complex habitats and higher mean annual temperature. Small mammal biomass was negatively associated with altitude (explained deviance: 37.9%) and positively associated with mean annual precipitation (explained deviance: 3.7%) and mean annual temperature (explained deviance: 0.1%), with a total explained deviance of 41.6% (Table 1). Finally, richness and diversity of small mammals was not explained by either of the variables assessed.

Using quadratic functions, small mammal richness could not be explained by any variable (Fig. 3, Supporting information). Diversity was explained by mean annual temperature and mean annual precipitation, showing a hump-shaped relationship, indicating that the lowest biodiversity of small mammals was recorded on sites with intermediate values of temperature and precipitation. Both variables explained 20.2% and 25.5% of total deviance respectively (Supporting information). Quadratic components of small mammal abundance did not explain more than 0.1% of total deviance, so abundance is better explained by linear components (Table 1). Biomass was also explained by soil hardness in a quadratic relationship (explained deviance 0.248), with the highest biomass values recorded on harder soil (Fig. 3-27, Supporting information). Finally, evenness was mostly associated with habitat complexity and mean annual temperature in both linear and quadratic components (Table 1; Fig. 3-10).

3.3. Regional scale

Evenness was positively associated with mean annual temperature (explained deviance: 76.4%) and mean annual precipitation (explained deviance: 22.3%), explaining a total of 98.6% of total deviance (Table 1). This suggests that more equitable assemblages occurred at sites with higher ambient temperature and higher mean annual precipitation, located principally in the northeast and middle east of Mendoza Province.

Species diversity was positively associated with temperature (explained deviance: 74.7%) and habitat heterogeneity (explained deviance: 3.1%), and negatively associated with mean annual precipitation (explained deviance: 21.2%), explaining a total of 98.9% of total deviance (Table 1). In this sense, most diverse assemblages were located in the northeast (sites with the highest mean annual temperature) and the middle east of Mendoza Province (sites with the highest habitat heterogeneity). Richness was negatively associated with habitat complexity, explaining 81.7% of total deviance (Table 1). Finally, abundance and biomass could not be explained by any of the variables assessed.

With respect to quadratic relationships, abundance was strongly

Table 1

Generalized Linear Models that are significant for each response variable at three scales (patch, locality and regional). Number of terms included in the model, percentage of total model explained deviance, Akaike Information Criteria (AIC), differences among AICs (Δ AIC), selection order and adjustment value of the model (p), are expressed in the table. * represents the significant variables of the model. Black bold indicates the selected model. References: Ppt: mean annual precipitation, T: mean annual temperature, Alt: altitude above sea level, Het: habitat heterogeneity, Compl: habitat complexity, Hab: habitat type.

Scale	Variable	Model	No. terms	%Expl. dev.	AIC	Δ AIC	Order	p (model)	
Patch	Abundance	Ppt(*) + T(*) + Alt(*)	3	17.4	55.92	0	1	0.007	
		Het + Ppt(*) + T(*) + Alt(*)	4	18.98	56.99	1.07	2	0.011	
		Hab + Ppt(*) + T(*) + Alt(*)	4	27.25	60.204	4.284	3	0.016	
Locality	Richness	Alt(*)	1	8.46	51.487	–	–	0.031	
		Ppt(*) + T(*) + Alt(*)	3	45.66	23.628	1.522	2	0.032	
	Abundance	Comp(*) + Ppt(*) + T(*) + Alt(*)	4	57.9	22.106	0	1	0.017	
		Het + Ppt + T(*) + Alt(*)	4	45.65	25.628	3.522	4	0.075	
		Het + Compl + Ppt(*) + T(*) + Alt(*)	5	58.27	24	1.894	3	0.04	
		Evenness	Compl(*)	1	29.5	21.911	2.201	3	0.02
		Compl(*) + T(*)	2	46.05	19.71	0	1	0.01	
		Compl(*) + Alt	2	41.12	20.893	1.183	2	0.019	
	Biomass	Compl(*) + Ppt	2	30.28	23.72	4.01	4	0.067	
		T(*) + Ppt(*) + Alt(*)	3	41.81	21.326	0	1	0.05	
Het + T(*) + Ppt(*) + Alt(*)		4	46.54	22.243	0.917	2	0.069		
Regional	Richness	Compl + T(*) + Ppt(*) + Alt(*)	4	42.52	23.166	1.84	3	0.103	
		Compl(*)	1	81.66	5.306	–	–	0.013	
	Evenness	T(*)	1	76.38	24.532	17.342	6	0.023	
		Heter(*)	1	64.011	35.284	28.094	7	0.056	
		Ppt(*) + T(*)	2	98.63	7.19	0	1	0.002	
	Diversity	Het + T(*)	2	91.97	12.981	5.791	4	0.023	
		Compl + T(*)	2	83.44	20.396	13.206	5	0.067	
		Compl + Ppt(*) + T(*)	3	98.8	9.039	1.849	2	0.018	
		Het + Ppt + T(*)	3	98.68	9.149	1.959	3	0.02	
		T(*)	1	74.69	203.11	192.11	5	0.026	
		Ppt(*) + T(*)	2	95.83	38.76	27.76	4	0.008	
		Het + Ppt(*) + T(+)	3	98.88	16.75	5.75	2	0.017	
		Compl + Ppt + T(*)	3	96.78	33.31	22.31	3	0.048	
		Het + Compl + Ppt + T(*)	4	99.87	11	0	1	0.053	

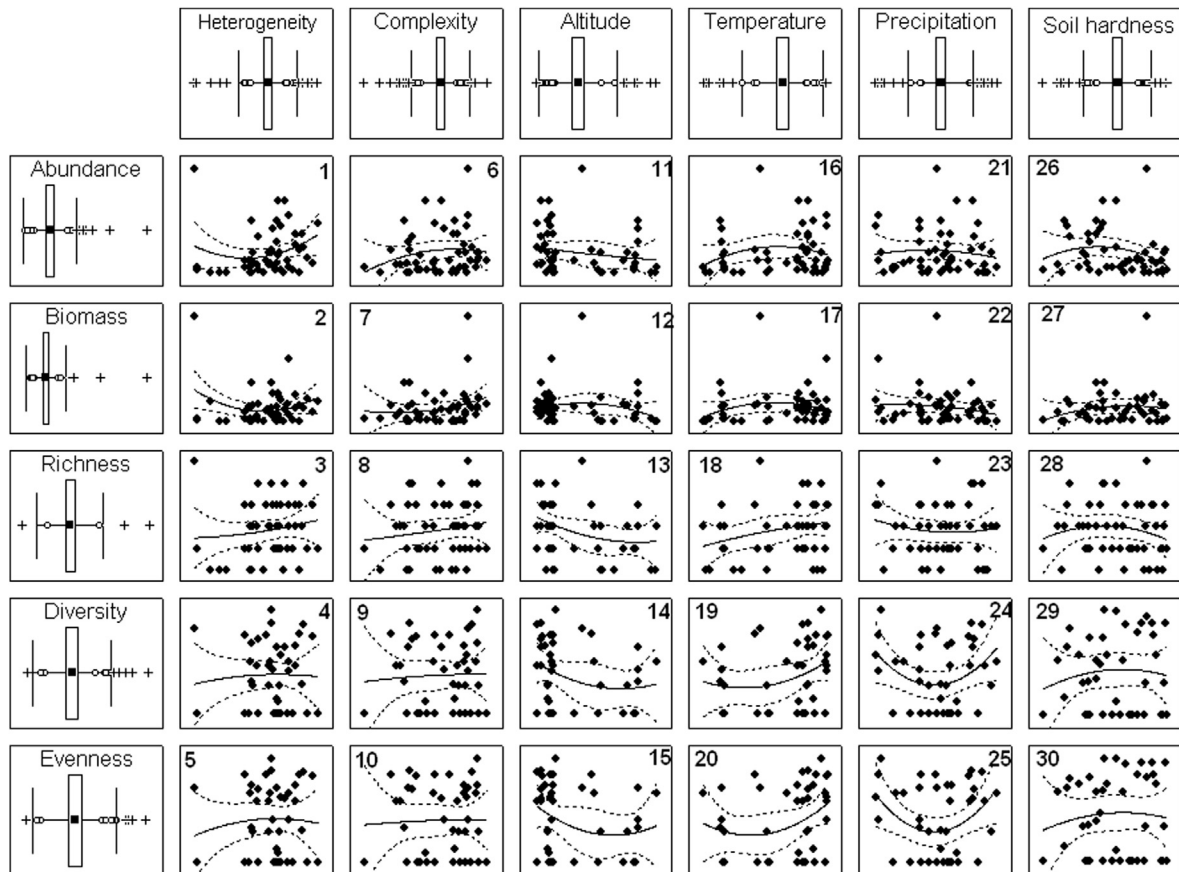


Fig. 2. Quadratic regressions at patch scale. Solid black line shows the function adjustment and dashed lines represent the 95% confidence intervals (upper and lower). Distribution of each variable is shown with a box-plot. ○ Mean, ... outlier, + extremes.

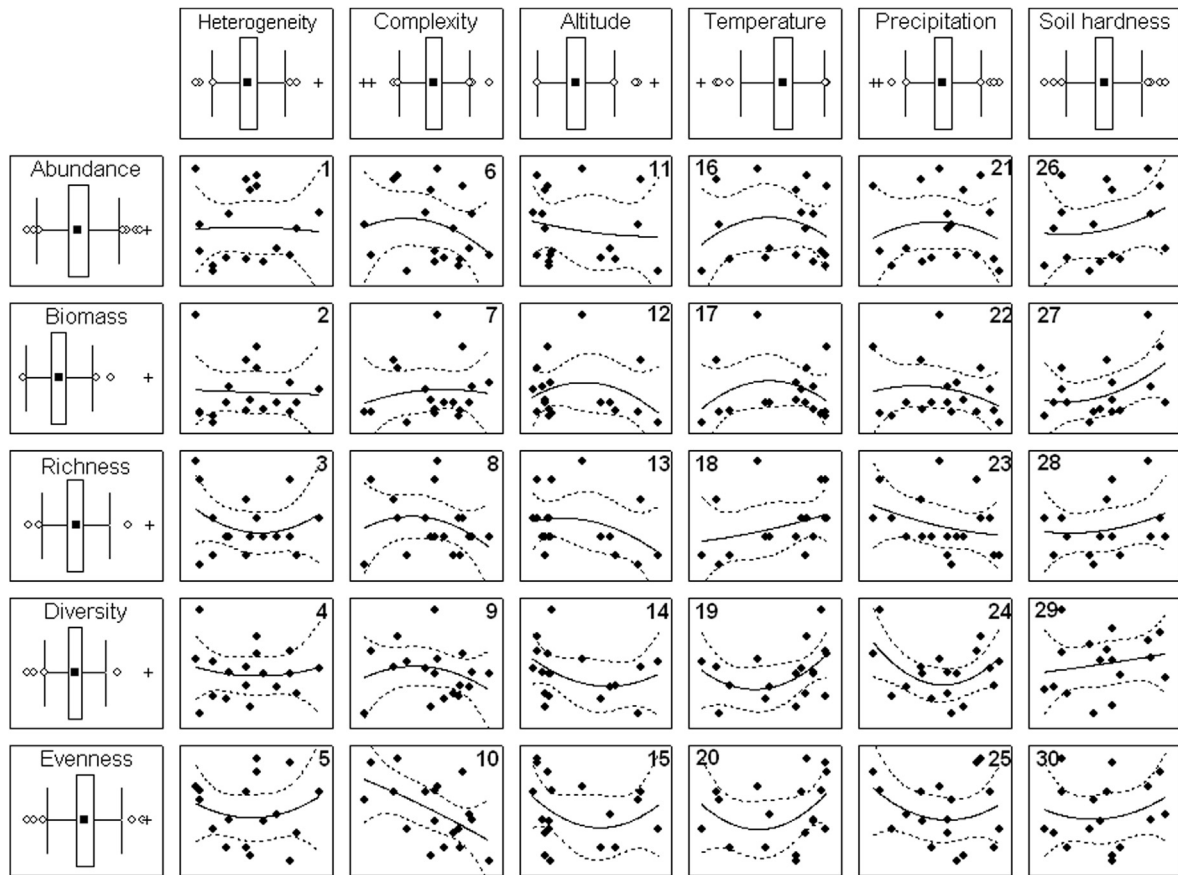


Fig. 3. Quadratic regressions at locality scale. Solid black line shows the function adjustment and dashed lines represent the 95% confidence intervals (upper and lower). Distribution of each variable is shown with a box-plot. ○ Mean, ... outlier, + extremes.

associated with soil hardness, showing a unimodal shape, with the highest small mammal abundance recorded on intermediate-soft soils (Fig. 4-26, Supporting information). Biomass, which did not show any linear association, was positively associated with habitat complexity; thus more complex sites had the highest small mammal biomass (Fig. 4-7, Supporting information). Species richness was mainly explained by habitat complexity in its linear component (Table 1) and habitat heterogeneity in its quadratic component (Fig. 4-3, Supporting information), adopting a hump-shaped curve with an adjustment of 61.9%, indicating that assemblages with lower richness values were located at intermediate habitat heterogeneity. Small mammal diversity was positively associated with habitat heterogeneity and mean annual temperature, both in linear and quadratic components (Fig. 4-4–19; Table 1; Supporting information). Moreover, the highest diversity was also recorded on sites located at low altitudes and with high values of soil hardness (showing an U shape) (Fig. 4-14–19; Supporting information). Evenness showed similar quadratic associations as diversity, with more even assemblages recorded on sites with higher mean annual temperature and habitat heterogeneity, lower altitude and lower soil hardness values (Fig. 4-5–15–20–30, Supporting information).

4. Discussion

Previous results on assemblage patterns in desert small mammals show an irregular scale dependence on biodiversity, meaning that the processes that regulate such patterns should be different at different spatial scales (Rodríguez and Ojeda, 2011, 2013). In this

paper we deal with exogenous factors as potential drivers in structuring assemblages of desert small mammals. We found that assemblage structure is strongly regulated by environmental drivers (e.g. temperature) at higher spatial scales (e.g. region) but there is a small effect at lower spatial scales (e.g. patch), supporting the hypothesis proposed by Loreau (2000). Moreover, environmental drivers vary in type and strength depending on the community estimator, showing a wide variety of responses and forms of association (unimodal, linear, hump-shaped), which highlights the importance of including several spatial scales, as well as several community estimators when dealing with assemblage processes.

The energy hypothesis states that higher energy availability (measured as temperature or food; Evans et al., 2005) provides a wider resource base to promote higher population abundances; and therefore, probability of extinction should be lower (Lande, 1993). It means that there should be a relationship between biomass or species abundance and some environmental variable (as a surrogate for energy availability). The shape of such relationship depends on the spatial scale, with hump-shaped relationships at small spatial scales and monotonic relationships at large scales (Wright et al., 1993). Our results support the energy hypothesis only at large spatial scales (i.e. regional). At patch scale we found a positive and linear relationship between abundance and climate drivers (i.e. mean annual temperature), whereas at higher spatial scales (regional) there was a positive relationship between biomass and habitat drivers (i.e. habitat complexity). Habitat complexity could be understood as an energy estimator, as well as climate drivers. An increase in habitat complexity (vertical structure) promotes the presence of higher animal biomass because

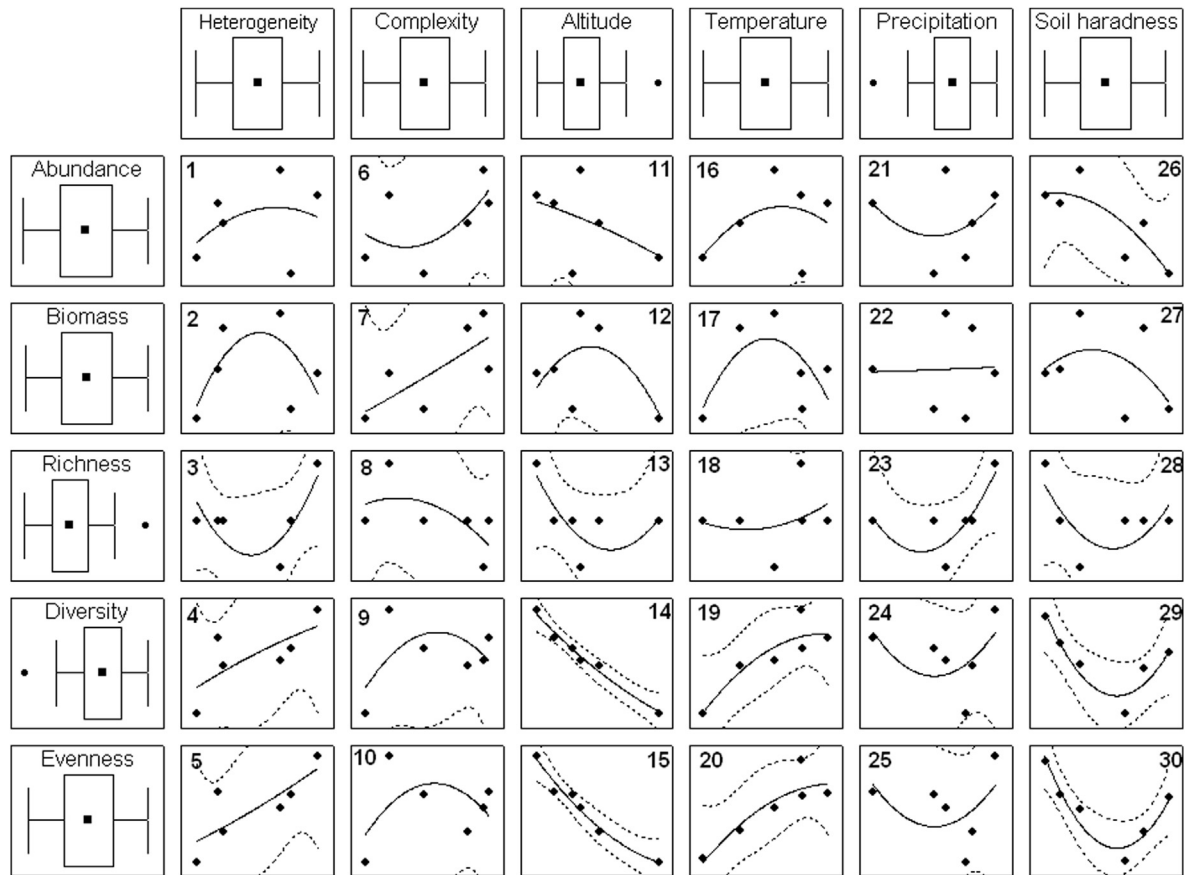


Fig. 4. Quadratic regressions at regional scale. Solid black line shows the function adjustment and dashed lines represent the 95% confidence intervals (upper and lower). Distribution of each variable is shown with a box-plot. ○ Mean, ... outlier, + extremes.

it promotes a higher number of potential niches to be occupied (August, 1983). In the Monte desert, for example, the marsupial *Thylamys pallidior* and the rodent *Graomys griseoflavus* take advantage of the structure of the tree and use both the horizontal and vertical spatial levels of the habitat. (Albanese et al., 2011).

A proper selection of the grain and extent of the spatial scale is important when searching for general processes regulating species diversity patterns. As Whittaker and Heegaard (2003) pointed out, keeping the grain, but not necessarily the extent of the spatial scale, should keep the sensitivity of the drivers that vary at the smallest spatial scales. Previous studies report that small mammal diversity in the Monte desert is positively associated to habitat heterogeneity at the patch scale (Corbalán, 2004). Nevertheless, and despite maintaining the same grain of spatial resolution, species diversity could not be explained by any habitat driver when the extent of the scale is doubled (Tabeni, 2006) or increases by more than 10 times (this paper). These results are opposed to the hypothesis proposed by Whittaker and Heegaard (2003), suggesting that other drivers, besides habitat complexity, promote patterns of coexistence in Monte desert small mammals at small spatial scales.

Previous studies have shown that, at small spatial scales, assemblage organization and coexistence in Monte desert small mammals can be explained by differential utilization of resources along habitat and diet niche axes (Ojeda et al., 2011; Rodríguez and Ojeda, 2014). Contrary to expectations, at the regional scale we found that species richness diminishes with habitat complexity. This could be explained by the auto-ecology of the regional species pool. In the Monte desert, most small mammals (*Eligmodontia typus*, *E. moreni*, *Calomys musculus*, *T. pallidior*, *Phyllotis*

xantophygus) use structurally simple habitats, or are indifferent to habitat complexity (*G. griseoflavus*, *Akodon* sp.), there being less species who prefer structurally complex habitats (*Akodon molinae*, *Salinomys delicatus*) (Corbalán, 2004; Corbalán and Debandi, 2006; Tabeni and Ojeda, 2005; Ojeda and Tabeni, 2009; Albanese et al., 2011; Albanese and Ojeda, 2012; Rodríguez et al., 2012). In some cases it was observed that there was a differential use of tree strata among species; for example, in the central Monte, desert rodents use the lower more than the upper parts of trees, whereas the marsupial *T. pallidior* is more selective, preferring the upper parts of trees (Albanese et al., 2011). Such vertical segregation could blur the relationship between species richness and habitat complexity.

Although precipitation could be expected to act as a driver in structuring species assemblages at the regional scale, we found no such relationship between species richness and precipitation. In previous studies of partitioning biodiversity in Monte desert small mammals, we found that several small mammal species are shared among regions with different precipitation regimes (Rodríguez and Ojeda, 2011). Nevertheless, an increase in species exchange does not merely imply an increase in species richness, but also a change in species identity (Legendre et al., 2005). In such relationship, the life span of species could play a major role. For example, in Chilean deserts, short-lived and long-lived species display opposite responses to rainy periods. Long-lived species of small mammals, such as caviomorph rodents, increase in number and remain relatively stable in higher abundances than short-lived sigmodontine rodents when rainfall events are more frequent (Meserve et al., 2011). It has been suggested that species with a short life span and high reproductive rates perceive each rainfall event as separate

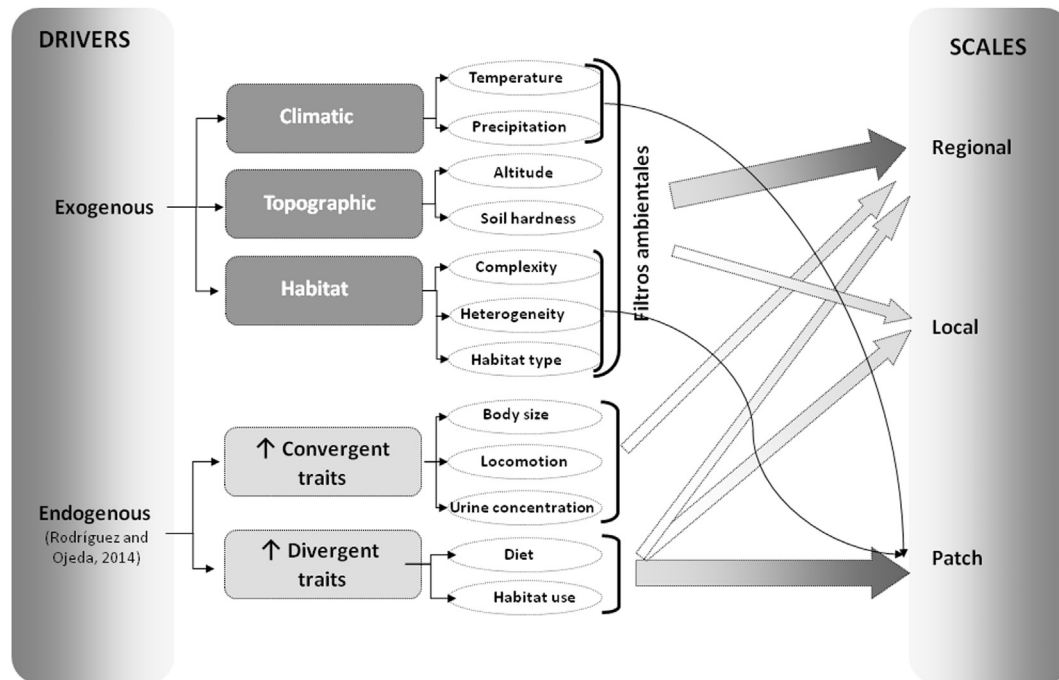


Fig. 5. Conceptual diagram of ecological drivers that influence small mammal assemblage structure in the Monte desert across different spatial scales. Thickness of the arrow indicates the intensity of the effect.

and independent rainfall pulses, whereas those species with low reproduction rates and a long life span show a cumulative response to rainfall pulses (Meserve et al., 2011). In our study system, most small mammal species mainly have short life spans and high reproductive rates, so the negative or null relationship between species richness and precipitation could be due to dominance of sigmodontine rodents among Monte desert small mammal assemblages.

Topographic variables mostly explain species diversity and evenness at the regional scale. Less diverse and less even assemblages occur at higher elevations and at intermediate soil hardness. The fact that species richness diminishes with altitude has been previously reported and mostly accepted (Stevens, 1992, and papers there in). Nevertheless, the shape of such relationship is still broadly discussed (Rahbek, 2005). In our system, elevation was strongly correlated with latitude ($r = 0.93$; $p < 0.0001$), with higher altitude sites being located at higher latitudes, in the south portion of Mendoza province. These places are located in the southwest portion of the Monte desert, bounded by the hyper-arid Payunia desert. On this region, mean annual temperature is very low and precipitation is more regular throughout the year, compared to the central portion of the Monte desert (Labraga and Villalba, 2009). Therefore, altitude (and consequently latitude) could be masking the effect of other drivers on small mammal assemblages.

Finally, irrespective of the group of explanatory variables, our results show that when the spatial scale increases, the degree of explicability of the exogenous factors also increases, with 17% of explicability at the patch scale (i.e. abundance) and 99% at the regional scale (i.e. diversity). On the other hand, endogenous drivers, such as interspecific interactions based on diet divergence and habitat use, had been recorded to be more relevant at the patch scale, with their importance diminishing from patch to regional scale (Ojeda et al., 2011; Rodríguez and Ojeda, 2014). Therefore, there is a relative variation in exogenous versus endogenous drivers that regulate the way small mammals are structured into assemblages as the spatial scale changes (Fig. 5). Our results fill up a

knowledge gap concerning ecological drivers of assemblage structure at intermediate spatial scales for small mammals of the Monte desert (Ojeda et al., 2011), and highlight the importance of dealing with multi-causal factors when searching for the ecological processes that structure assemblage patterns.

Acknowledgments

We want to thank all the field assistants, whose help made this project possible: Elias Muriel, Miriam Benzaquín, Lucia Boiani, Lorena Padula, Franco Minetti, Verónica Chillo, Carla Cuende, Pablo Cuello, Andrés Ligrone, Viviana Seitz, Diego Ferrer, Paula Costilla, Rosa Perello, Sigrid Nielsen, Leandro Álvarez, Verónica Soñez, M. Eugenia Arias, Andrea Donello, Daniel Hernandez, Soledad Albanese and Agustina Ojeda. Also, the Dirección de Áreas Naturales Protegidas de la Provincia de Mendoza and IADIZA gave us all the required sampling permits and the owners of private ranches allowed us to work on their properties and gave us a place to stay. We appreciate the insightful comments on the manuscript made by Soledad Albanese, and Fernanda Cuevas. Finally, we want to thank Nelly Horak for helping us with the English version of the manuscript. This project was supported by Idea Wild, Rufford Small Grant for Nature Conservation RSG-41.05.07, SECYT PICT-11768, 25778 and CONICET PIP-5944, 2884.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2015.10.012>.

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