



Original article

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



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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 $<10^{\circ}$ C in winter to $>20^{\circ}$ 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 ($96,000 \text{ km}^2$) (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 ($4 \text{ m} \times 250 \text{ m} = 0.1 \text{ ha}$) 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 $16,000 \text{ km}^2$.

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:

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