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Scaling functional diversity of small mammals in desert systems

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Abstract

Although scaling biodiversity is a common topic in ecology, scaling functional biodiversity is a major theoretical and analytical challenge, mainly because trait differentiation and regulating processes occur at different spatial scales. Here, we propose a method to scale functional biodiversity by comparing the relative dominance of convergent versus divergent functional traits across environmental gradients. Particularly, in highly variable systems such as deserts, one would expect species convergence in the use of an abundant resource through niche filtering, promoting functional redundancy (stability hypothesis), but at which spatial scale? We tested this approach using small mammal assemblages of the Monte Desert (Argentina, South America) and found that divergent traits are dominant on smaller spatial scales, whereas convergent traits are present only at the highest spatial scale. Functional complementarity was recorded at the community and meta-community levels, suggesting that niche partitioning is the main regulating process and diet the major divergent trait. At regional scale, divergent traits were also present, indicating that biodiversity is also regulated by niche filtering. Finally, we found that the stability hypothesis cannot be generalized for desert systems but depends on the spatial scale. This novel approach offers new insights into the search for an integrative perspective on functional biodiversity.

Introduction

To understand the processes that regulate community structure patterns, ecologists have sought ecological rules that not only govern assemblage structure and the function of ecological communities but that can also be used to predict the response of a community when facing a change event (Weiher & Keddy, 2001). It has been almost 4 decades since the first community assembly rule was described (Diamond, 1975), and the new ecological approach on functional traits allows ecologists to go deeper into the understanding of assemblage processes.

As individuals only interact at smaller spatial scales, most functional approaches related to the processes of assemblage patterns have been restricted to the patch or locality scale (Pillar *et al*., 2009). Functional biodiversity across spatial scales has only been evaluated by De Bello *et al*. (2009), who used the Whittaker (1975) approach of multiplicative partitioning of biodiversity into alpha, beta and gamma functional diversity (FD). Despite their remarkable work on scaling functional diversity, they restricted it to a single functional trait (De Bello *et al*., 2009). Nevertheless, because ecological processes do not respond to a single functional trait, but to the interaction of several traits, it is necessary to have a more inclusive analytical methodology. So then the question is, how do we evaluate functional diversity across spatial scales?

A recent approach proposed by Pillar *et al*. (2009) could shed light on our question. They proposed a simple methodology to measure the relative dominance of convergent versus divergent traits for a plant community. Their methodology can be applied independently of the spatial scale and includes more than one functional trait. Basically, the dominance of one or other types of functional trait at different spatial scales could shed light on which processes regulate functional diversity across spatial scales. The niche filtering process could act as the main regulating process at higher spatial scales, leading to a potential trait convergence among coexisting species (Díaz *et al*., 2007; Resetarits & Chalcraft, 2007). However, because coexisting species do not show exactly the same ecological traits, limiting similarity and competitive exclusion (MacArthur & Levins, 1967) may favor the presence of divergent traits (Pillar & Duarte, 2010) mainly at local scale (Resetarits & Chalcraft, 2007).

In highly variable systems such as deserts, and on the basis of the environmental stability hypothesis, one would expect species to converge in their use of an abundant resource, thereby promoting redundancy of functional traits (Wiens, 1977; Cardinale, Nelson & Palmer, 2000). On the contrary, competition in stable environments would probably regulate assemblage structure by increasing functional structure through niche segregation (Schoener, 1982). On the basis of this hypothesis, deserts offer a perfect scenario to test how functional diversity varies among spatial scales in variable environments. Such variability could be reflected in time or space. Temporal variability had been mostly associated to precipitations with consequent intermittent pulses of resources and finally temporal variability of population abundance. Spatial variability had been mostly associated to habitat selection, with species abundance varying among habitats with different heterogeneity (Letnic & Dickman, 2010; Ojeda, Tabeni & Corbalan, 2011). Particularly, we used desert small mammals as a case study because assemblages are simple but diverse and species are conspicuous and abundant (Shenbrot, Krasnov & Rogovin, 1999).

Functional diversity was previously evaluated on desert's small mammals by using Fox's assemblage rule, which states that: 'there is a much higher probability that each species entering a community will be drawn from a different functional group (genus or other taxonomically related group of species with similar diets) until each group is represented, before the cycle repeats' (Fox, 1989). According to Fox, the underlying mechanism that promotes species coexistence is competitive exclusion because of the presence of only divergent evolutionary traits (Fox, 1989). Nevertheless, this rule can be applied just for one functional trait at a time, the same limitation as in the approach proposed by De Bello *et al.* (2009). Despite the fact that Fox's rule and Pillar's methodology have the same theoretical background, the first was only used on desert's small mammals and the second mostly in plants. Here, we intend to verify the results of the methodology of Pillar *et al.* (2009) using Fox's assembly rule.

We propose to use the relative dominance of convergent versus divergent functional traits across environmental gradients (Pillar *et al.*, 2009) to evaluate the way in which functional biodiversity scales in space. Moreover, determining which traits are convergent or divergent for different environmental filters across a gradient of spatial scales could shed light on the processes that structure desert assemblages as well as on the strength of the stability hypothesis. Finally, our research revolves around the following questions: (1) How does dominance of convergent or divergent functional traits vary among different spatial scales?; (2) Is there functional redundancy or complementary among desert small mammals?; (3) Do desert small mammal assemblages support the environmental stability hypothesis? And if so, at which spatial scale?; (4) Can this approach be used to understand scaling patterns of functional diversity?

Materials and methods

Study area, scaling 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 varies from 50 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).

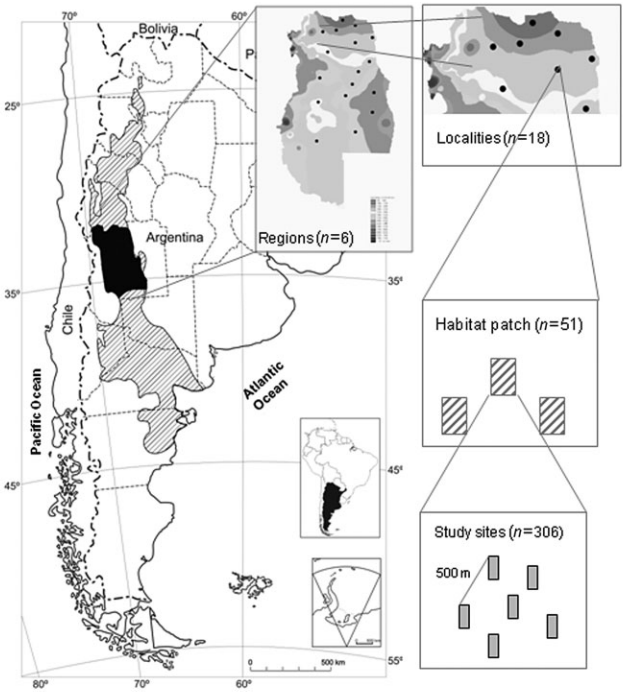

Figure 1 Study area in the Monte Desert (Argentina, South America) and scaling sampling design. Dashed lines delimit the Monte Desert biome; the black spot is the location of the central portion of the Monte Desert where sampling was conducted; and the number of sampling units for each spatial scale is indicated in brackets.

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 six 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 of Scheiner *et al.* (2000). Sample extent (geographical space

Table 1 Functional traits and their characteristics used to estimate functional diversity (RAO index) and richness (FD index)

Trait	Type	Categories
1. Diet	Categorical – numerical	Insectivorous – granivorous – folivorous – omnivorous – halophytic plants
2. Urine concentration	Categorical	High (>800 mOsm L^{-1}) – medium (between 300 and 790 mOsm L^{-1}) – low (<300 mOsm L^{-1})
3. Ratio of kidney inner medulla to cortex	Categorical	Very high (>9) – high (between 6 and 9) – medium (between 4.5 and 6) – low (<4.5)
4. Torpor	Categorical – binary	Yes – no
5. Locomotion	Categorical – binary	Biped – quadruped
6. Locomotion	Categorical – binary	Scansorial – cursorial
7. Fossoriality	Categorical	Totally fossorial – semi fossorial – no fossorial
8. Activity period	Categorical – binary	Day – night
9. Sociability	Categorical – binary	Yes – no
10. Body size (tail length/body length)	Categorical	A (>1.4 cm) – B (between 1.2 and 1.4 cm) – C (between 1.2 and 1.1 cm) – D (between 1.1. and 1 cm) – E (between 1 and 0.89 cm) – F (<0.8 cm)
11. Body weight	Categorical	A (<15 g) – B (between 15 and 30 g) – C (between 30 and 55 g) – D (>55 g)
12. Habitat use	Categorical – Numerical	*Prosopis* woodlands – *Larrea* shrublands – other shrublands – sand dunes – salt flats – pampas grasslands

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.

Trapping was performed between September 2005 and June 2008, with total sampling effort being 23 000 traps per night. Sampling effort was focused mainly between January and June of each year because Monte desert small mammals have their abundance peak 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 among the regional scale. Small mammal sampling was conducted with live-capture Sherman traps. 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. Captured animals were identified to species level, marked with picric acid for individual identification and then released.

This sampling design allows understanding of these spatial scales on an ecological meaning. The patch scale was related to a community level since small mammals mainly interact at this spatial level. The locality scale allows understanding of the meta-community structure because it includes several habitat types among which small mammal populations interact. The regional scale includes an upper meta-community level, referring to the regional pool of species, where local communities do not effectively interact with each other. From here on, we will refer to the three spatial scales as the three organization levels in order to approach the ecological meaning of the spatial scales: patch = community, locality = meta-community and region = regional species pool.

Functional trait selection and data analysis

A functional trait is defined as a characteristic of an organism that is relevant to its effect on ecosystem functioning (Díaz & Cabido, 2001; Chillo & Ojeda, 2012). Particularly, selected traits are those that influence the processes of nutrient cycling throughout the capture, use or transformation of resources (Flynn *et al*., 2009) and for which there is available information for all the captured species. For example, diet, body size and weight are related to the type of resource (food or habitat) and the quantity of it that each species could deal with. Activity patterns such us torpor, locomotion, fossoriality, activity period, habitat use and sociability are functional traits related to temporal and spatial distribution of resources (Flynn *et al*., 2009).

Here, functional traits were considered at the species level because we lacked information of each trait value for each individual of the 53 sampled communities. Therefore, only the most conserved functional traits at the species level were included, meaning those with little or no intra-specific variation. Functional traits and their characteristics are shown in Table 1. Bibliographical reports were used for traits 1–9, and the IADIZA Mammal Collection database was used for traits 10 and 11. Habitat use, trait 12, was collected from sampled individuals.

Scaling patterns of trait convergence and divergence were evaluated using the technique proposed by Pillar *et al*. (2009). Trait-convergence assembly pattern (TCAP) and trait-divergence assembly pattern (TDAP) were estimated at three structural levels: community (patch), meta-community (locality) and regional species pool (regional). Because habitat heterogeneity and precipitation gradients are among the major features of the Monte Desert (Morello, 1958), we used both gradients to test convergence and divergence patterns. Habitat heterogeneity data were obtained from Rodríguez & Ojeda (2011) and the precipitation gradient followed the one proposed by PAN (Programa de Acción Nacional de la Lucha

Table 2 Functional traits that maximized processes of convergence or divergence along two environmental gradients (heterogeneity and precipitation) across different organization levels (community, meta-community and regional species pool)

		Heterogeneity pattern		Precipitation pattern	
Level		TDAP (divergence)	TCAP (convergence)	TDAP (divergence)	TCAP (convergence)
Community	Functional traits	Diet, cortex/medulla, body size	–	Diet, torpor	–
	ρ (**TE**) **conv.**	0.1046	0.2488	0.1026	0.2032
	P	0.253	0.101	0.346	0.125
	ρ (**XE.T**) **div.**	**0.31**	0.1267	**0.2845**	0.1379
	P	**0.009**	0.787	**0.05**	0.077
Meta-community	Functional traits	Diet, locomotion race, weight	–	Diet	–
	ρ (**TE**) **conv.**	0.1218	0.1881	0.3222	0.295
	P	0.774	0.988	0.074	0.113
	ρ (**XE.T**) **div.**	**0.1705**	0.0589	**0.4729**	0.2995
	P	**0.001**	0.87	**0.008**	0.074
Regional species pool	Functional traits	Body size, torpor	Body size	Body size, scansorial locomotion	Body size, scansorial locomotion
	ρ (**TE**) **conv.**	0.2279	**0.9132**	0.227	0.228
	P	0.973	**0.012**	0.121	0.121
	ρ (**XE.T**) **div.**	**0.9023**	0.3667	**0.7765**	**0.7765**
	P	**0.034**	0.956	**0.003**	**0.003**

Significant values ($P < 0.05$) are shown in boldface and ρ corresponds to the matrix correlation values.
TCAP, trait-convergence assembly pattern; TDAP, trait-divergence assembly pattern.

contra la Desertificación; Naumann & Madariaga, 2003). SYNCSA program was used for the analyses, available online for free at http://ecoqua.ecologia.ufrgs.br/.

Testing Pillar's methodology using assembly rules

Fox's assembly rule was analyzed to verify the results of the methodology of Pillar *et al.* (2009). We tested it at the community (patch) and meta-community levels (locality) only because individuals or populations only interact at these structural levels (spatial scales). Here, the idea is to corroborate that the trait-divergence assemblage patterns proposed by Pillar are mostly the same idea as Fox's rule. Of the 12 functional traits listed previously, only 3 (diet, habitat use and body weight) were used to test Fox's rule because they were previously evaluated on other desert's small mammal assemblages, allowing for comparisons to be made. The numbers of assemblages (or sites) that followed or did not follow Fox's rule were estimated and contrasted using the chi-squared test.

Redundancy and complementarity

We used two approaches to test whether species abundance could influence assemblage structure: (1) functional; (2) specific; and estimated richness and diversity in both cases. We estimated the number of species present in each assemblage to measure species richness and Shannon's diversity index to calculate species diversity. Because there are a lot of ways to measure functional diversity, we followed the classification proposed by Mouchet *et al.* (2010), where the FD index was used for functional richness (Petchey & Gaston, 2002) and the RAO index was used for functional diversity (Rao, 1982; Botta-Dukát, 2005). The RAO index was estimated using the free online macro available at http://botanika.bf.jcu.cz/suspa/FunctDiv.php (Lepš *et al.*, 2006). The FD index was estimated in the R program (R.2.13) using the Xtree package (Petchey & Gaston, 2002).

We performed a linear regression model between FD and species diversity and between functional richness and species richness to test if species are redundant or complementary in their function within the ecosystem. If the regression slope is ≤1, both variables have little or no influence on each other, and so there is no redundancy. Conversely, if the regression slope is >1, then the species assemblage shows redundancy.

Results

Scaling patterns of trait convergence and divergence

Only significant functional traits that maximized divergence between small mammals were found at the community and meta-community levels, for both the precipitation and the heterogeneity gradients. Diet was the only significant trait at both levels (community and meta-community) and on both gradients (heterogeneity and precipitation) (Table 2). At the regional species pool level, results varied depending on the gradient considered. Only divergent traits (body size and locomotion) were significant for the precipitation gradient,

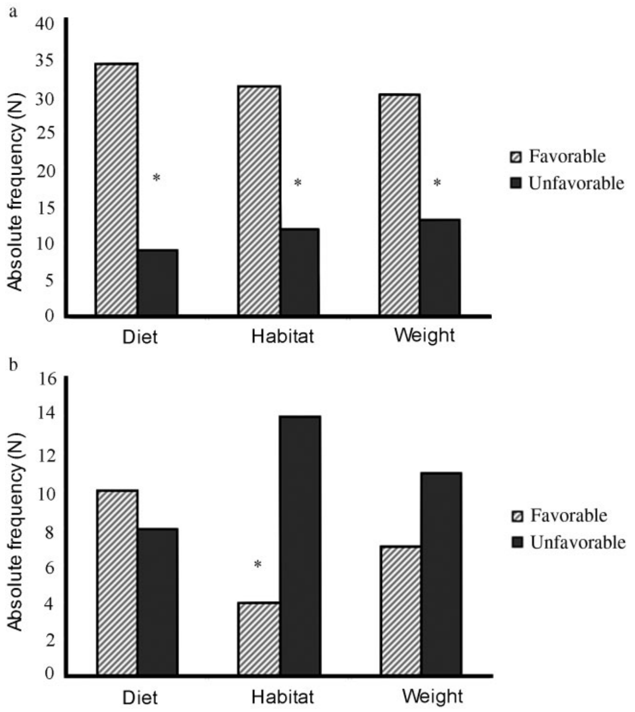

Figure 2 Fox's rule tested at (a) the community level and (b) meta-community level. The asterisk (*) represents significant differences, between favorable and unfavorable assemblage states, with $P < 0.05$.

whereas a convergent trait (body size) at the higher organization level was significant for the heterogeneity gradient (Table 2).

Testing Pillar's methodology using assembly rules

At the community level, the number of assemblages that followed Fox's rule was significantly higher than the number of assemblages that did not follow it for diet, habitat use or body weight [$\chi^2 = 14.53$, $P < 0.0001$, degrees of freedom (d.f.) = 1; $\chi^2 = 8.39$, $P = 0.003$, d.f. = 1; and $\chi^2 = 6.72$, $P = 0.009$, d.f. = 1, respectively] (Fig. 2a). At the meta-community level, neither functional trait (diet or body weight) was significant for Fox's rule ($\chi^2 = 0.222$, $P = 0.637$, d.f. = 1 and $\chi^2 = 0.8889$, $P = 0.346$, d.f. = 1, respectively), whereas the functional trait habitat use showed significantly more unfavorable than favorable states ($\chi^2 = 5.556$, $P = 0.018$, d.f. = 1) (Fig. 2b).

Redundancy and complementarity

A linear and positive relationship between species and functional diversity ($n = 43$, $R^2_{\text{adj}} = 0.86$, $P < 0.0001$) (Fig. 3a) was found with a regression slope of $b = 0.34$. The same pattern was found for species and functional richness ($n = 51$, $R^2_{\text{adj}} = 0.91$, $P < 0.0001$) (Fig. 3b), with a regression slope of $b = 0.27$.

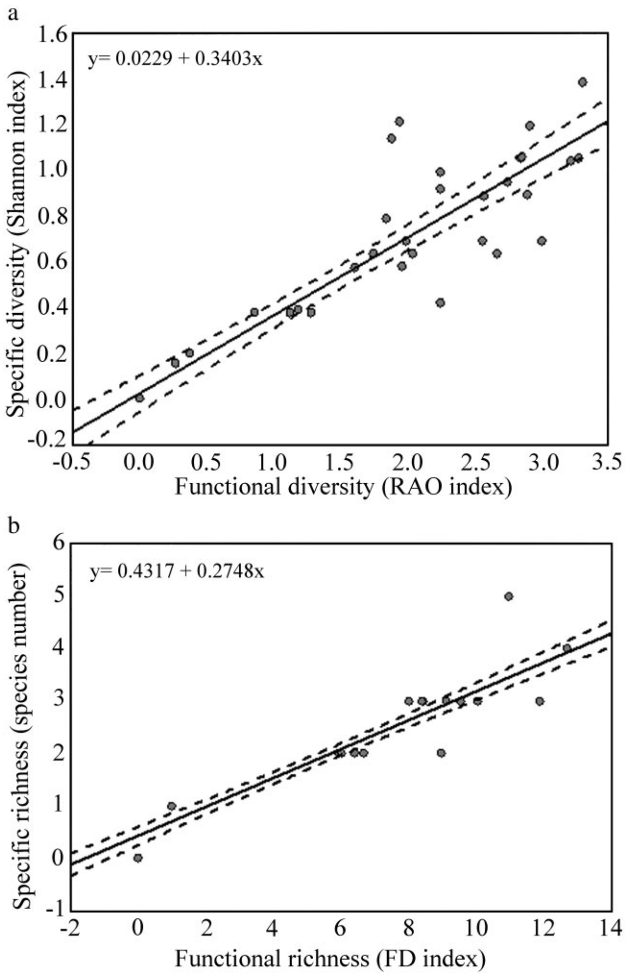

Figure 3 Linear regression between species and functional diversity (a) and between species and functional richness (b) at the community level. Dashed lines represent 95% confidence intervals.

Discussion

Our study shows that divergent traits are dominant on smaller spatial scales, whereas convergent traits are present only at regional spatial scales. These results suggest that niche partitioning is the main process regulating communities and meta-communities, and that regional species pool is mainly regulated by niche filtering. Results using Fox's assembly rule support the idea that partition on the trophic niche axis is one of the main regulating factors at the community level. Probably because of this, complementarity is the dominant mechanism through which desert's small mammals enhance ecosystem functioning. Finally, our results reveal that the acceptance of the stability hypothesis for desert systems depends on the spatial scale considered. As regards our posed questions:

(1) How does the dominance of convergent or divergent functional traits vary among different spatial scales (organization levels)?

Previous studies on the small mammals of the Monte Desert show an irregular dependence of biodiversity with different spatial scales (Rodríguez & Ojeda, 2011), meaning that alpha and beta's biodiversity contributes in a nonlinear way to regional biodiversity along the gradient of spatial scales (Gering and Crist, 2002). These results coupled with an increase in nested patterns on higher spatial scales (Rodríguez & Ojeda, 2013) indicate that the ecological processes that drive community structure are different at each spatial scale. Our results on differential dominance of convergent or divergent traits when scaling functional biodiversity support these studies. Divergent traits were dominant at the community and meta-community levels, whereas convergent traits were so at the regional species pool organization level. This pattern remained mostly stable regardless of the environmental gradient considered.

At the community level, Fox's rule was strongly supported by our data, segregating niche on the basis of three functional traits (diet, habitat and body weight), this segregation being possible because of the dominance of divergent traits in the species composing the assemblages (Fox, 1989). Therefore, at the community level, both analyses support the idea that the small mammal assemblages of the Monte Desert are organized according to niche segregation (Ojeda *et al*., 2011) and that there is an absence of convergent traits at the community and meta-community organization levels. At the meta-community level, Fox's rule was not significant for diet, body size or habitat use. This could be due to the nested structure of small mammal assemblages (Rodríguez & Ojeda, 2013), with a generalist species being the most abundant and widely distributed, accompanied by other subordinate and more narrowly distributed species. In these assemblages, more abundant species are mainly habitat generalists, and so patch differences are diluted at the meta-community scale.

Diet was the only significant trait present in both environmental gradients (heterogeneity and precipitation) and on both organization levels (community and meta-community). Previous studies on the small mammals of the Monte Desert report trophic segregation among vesper mouse *Calomys musculinus*, silky mouse *Eligmodontia typus*, grass mouse *Akodon molinae*, leaf-eared mouse *Graomys griseoflavus* and desert mouse opossum *Thylamys pallidior* (Giannoni *et al*., 2005; Albanese, Dacar & Ojeda, 2012). Nevertheless, species such as salt flat mouse *Salinomys delicatus*, Monte gerbil mouse *Eligmodontia moreni*, red vizcacha rat *Tympanoctomys barrerae* and Patagonian leaf-eared mice *Phyllotis xanthopygus* have never been included in this type of community analyses. Our results show that these species segregate the trophic niche to allow coexistence.

At the regional scale, we found both convergent and divergent traits, depending on the analyzed environmental gradient. Body size was the only convergent trait in the heterogeneity gradient, meaning that assemblages are constituted by species with similar body size within different habitat types. The precipitation gradient showed body size as a divergent trait, meaning that species that occur within the same precipitation range show different body sizes. Among divergent traits, diet was also important at the regional scale, for both the heterogeneity and the precipitation gradients, indicating that diet is the major divergent trait in structuring small mammal assemblages of the Monte Desert. These results agree with those reported for other desert small mammals, where diet segregation is the main factor structuring assemblages of desert systems (Fox, 1987; Kelt *et al*., 1996; Ganzhorn, 1997; Ojeda *et al*., 2011, and papers therein).

(2) Is there functional redundancy or complementarity among desert mammals?

The dominance of divergent traits on assemblage structure is supposed to promote the presence of species with complementary trait values, leading to the absence of functional redundancy (Díaz & Cabido, 2001). The results of the regressions between species and functional diversity and species and functional richness support this hypothesis. According to Petchey *et al*. (2007), this relationship clearly shows a lack of intrinsic redundancy, mainly because the number of species at the community level is too low to allow redundancy (in our study, five species maximum). The loss of any one small mammal species in the Monte Desert can therefore imply a direct change in its community structure (Resetarits & Chalcraft, 2007). Lack of functional redundancy has been recorded previously for a large variety of taxa (Díaz, Cabido & Casanoves, 1999; Loreau, 2004; Farias & Jaksic, 2007; Petchey *et al*., 2007; Resetarits & Chalcraft, 2007; Thibault, Ernest & Brown, 2010), with the presence of redundancy being less frequent (Micheli & Halpern, 2005).

Functional complementarity has been previously explained by two types of mechanisms: ecological or evolutionary. Proposed ecological mechanisms, mainly related to niche theory, are limiting similarity (MacArthur & Levins, 1967), competitive exclusion (Schoener, 1982), diffuse competition (Fox, 1981), competition by interference (Fox & Pople, 1984), opportunism (Rotenberry & Wiens, 1980; Farias & Jaksic, 2007) and nonrandomly distributed resources (Fox & Kirkland, 1992). Likewise, allopatric speciation associated with distributional range patterns has been proposed as an evolutionary mechanism that could explain functional complementarity (Bowers & Brown, 1982).

In arid lands, species are expected to make an opportunistic use of resources, mainly by using them according to their availability (Noy-Meir, 1973, 1979; Meserve, 1981; Jaksic, 1989). Even though our results do not allow us to discern which processes promote functional complementarity, previous reports on small mammal assemblages of the Monte Desert suggest that it is mainly associated with the precipitation regime (Corbalán, 2004; Albanese, 2010). In small mammal assemblages of the Monte Desert, opportunism is assumed to be species-dependent because each species perceives environmental variability in a different way and therefore also respond to it in a different way (Campos, 1997; Tabeni, 2006; Albanese *et al*., 2012). This type of species-dependent opportunism has also been also recorded in other desert systems, such as in primary consumer communities in Australia (Morton *et al*., 2011) and secondary consumer communities in Chile (Farias & Jaksic, 2007).

(3) Do desert small mammal assemblages support the environmental stability hypothesis? And if so, at which spatial scale or organization level does it occur?

According to the environmental stability hypothesis, unstable environments such as deserts would be expected to support assemblages mainly dominated by convergent traits related to the use of the most abundant and stable resources (Wiens, 1977). Previous studies in the semi-desert biome of central Chile (South America) reject this hypothesis for the vertebrate predator assemblage, mainly because divergent traits were found to be dominant (Farias & Jaksic, 2007). Our results at the lower organization levels reject the environmental stability hypothesis because of the presence of only divergent traits. Nevertheless, the presence of convergent traits at the regional species pool level in the small mammals of the Monte Desert supports the environmental stability hypothesis. This means that the acceptance or rejection of this hypothesis is directly related to the spatial scale or organization level considered. Similar conclusions were reached for plant communities, highlighting the importance of spatial scale when dealing with functional traits (Meinzer, 2003).

(4) Can we use this approach to understand scaling patterns of functional diversity?

All methods used here to disentangle the underlying mechanisms that regulate the way assemblages are constructed were consistent with each other. Nevertheless, the approach of Pillar *et al*. (2009) not only provided more detailed information on the relative importance of each functional trait but also allowed scaling functional biodiversity across several spatial scales along environmental gradients. Finally, this approach for scaling functional diversity offers new insight into the analysis of assemblage and coexistence patterns. Partitioning functional diversity among different organization levels offers a valuable tool when addressing questions related to an integrative perspective of functional assembly rules. Despite the difficulty of obtaining all of the input data for such multivariate analyses, we strongly encourage scientists to adopt such a multifactorial view when analyzing assemblage structure and function.

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