Connecting landscape structure and patterns in body size distributions

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Understanding the interaction between community structure and landscape structure represents a pressing theoretical challenge of great applied importance considering the increasing structural modification of ecosystems through habitat loss and fragmentation. Dispersal ability and energetic demands coupled to body size determine the landscape structure experienced by an organism, which could essentially be fragmented for small individuals but continuous for large ones. Although discontinuities in species assemblages have been predicted and detected, no explicit association between habitat structure and body size distributions has been demonstrated. In this contribution, we propose that body size structure in local communities should reflect such different perceptions of landscape structure. To this end, we explore this association in a simple metacommunity located in the Atacama Desert, in northern Chile. Using graph theory we found that species of different size and trophic position (carnivores and herbivores) perceive the landscape at contrasting spatial scales. In each community (n = 31) we determined the observed and the expected body size distributions – in a random sample from the metacommunity of 18 727 individuals –, which allowed us to identify the body sizes at which an overrepresentation or underrepresentation of individuals occur. Such aggregations and discontinuities in body sizes for herbivores. Our study shows, for the first time, an empirical connection between the spatial distribution of communities, their local attributes, and the existence and locations of discontinuities and aggregations in body size distributions.

Landscape structure has been recognized as of great importance for understanding population dynamics (Levins 1969, Hanski 1999) and community structure (MacArthur and Wilson 1967, Hubbell 2001, Holyoak et al. 2005). The movement of individuals between patches connects local communities to the whole metacommunity, determining species incidence and communities' diversity. In this context, two key components of landscape structure that could affect the dispersal of individuals and their persistence in the metacommunity are configuration and geometry (Turner et al. 2001). Configuration refers to the spatial arrangement of patches accounting for their position in relation to the dispersal of individuals through the whole network of patches. The relevance of this attribute in metacommunities has recently been highlighted (Urban and Keitt 2001, Economo and Keitt 2008, 2010, Minor et al. 2009). On the other hand, patch geometry refers to attributes of patches such as area, perimeter, and heterogeneity, which are known to affect community attributes such as species diversity (Ricklefs and Schluter 1993, Rozenweig 1995, Morin 1999). Interestingly, recent advances in community ecology have highlighted a main role of individual dispersal flow at the local and metacommunity scale as a determinant of patterns of distribution and abundance of species (Hubbell 2001, Keddy and Weiher 2004, Estrada and Bodin 2008, Economo and Keitt 2008, 2010). It should be noted that these theories draw attention to the role of landscape configuration, in an ecological theory essentially focused on geometric attributes.

The landscape structure experienced by one individual is essentially determined by its body size (McCann et al. 2005). The body size of a given organism determines the maximum distance it can travel, at which speed, and the maximum time between meals (Peters 1983, McNab 2002, Brown et al. 2004). In addition, larger animals could occupy upper trophic positions (Arim et al. 2007, 2010). Carnivores of relative big size have large energetic demands (McNab 2002). However, within a single patch the low efficiency in resource transfer between trophic links determines a reduction in available energy, making movement between patches a requisite for the organism's persistence (McCann et al. 2005, Arim et al. 2010). These biological attributes tied to body size have a deep effect on the perception of landscape configuration, which could essentially be disconnected for small individuals but continuous for larger ones (Keitt et al. 1997, Urban and Keitt 2001).

Body size distributions in local communities should reflect such different perceptions of the landscape structure. The smaller and larger organisms, particularly carnivores, are the most sensitive individuals to the amount of resources available in a patch (Brown et al. 1993, Marquet and Taper 1998, Burness et al. 2001). The representation of these size classes in local communities could be affected by the immigration of individuals from the metacommunity. This predicts a positive association between the flow of extreme-size individuals and their representation in the community. Consequently, connected patches could have more individuals in extreme size classes than would be predicted by a random sample from the metacommunity, a pattern that should be stronger in carnivores, which tend to be larger and dispersed over longer distances (Peters 1983). Similarly, it has been postulated that discontinuities in resource availability along scale gradients determine the occurrence of discontinuities and aggregations in body size distributions (Holling 1992). As the distance between a patch of habitat and the rest of the system increases, individuals of smaller size classes will be underrepresented in the local community. In this sense, many studies have found discontinuous patterns in body size distributions in spatially heterogeneous systems (Gunnarsson 1992, Szabó and Meszéna 2006, Rabosky et al. 2007). However, the explicit association between body size structure, trophic behavior and the discontinuous spatial structure of the landscape has not been adequately addressed.

In the Atacama Desert, in northern of Chile, the interplay between fog advection by wind and local topography gives rise to a landscape composed of isolated monospecific patches of the bromeliad Tillandsia landbeckii (Borthagaray et al. 2010, Fig. 1). These patches of varying connectivity and area are distributed across the landscape and embedded in a sand matrix without vegetation. In addition, the interception of the fog-water input by the plant biomass produces a characteristic banded vegetation pattern within patches (Fig. 1, Borthagaray et al. 2010). These bands have different widths, interband distances and heights. Animal communities in this area are composed mainly of arthropods (except for one species of lizard and one species of gecko), and display a wide range of body sizes spanning four orders of magnitude. Thus, animals with different spatial requirements, dispersal abilities and perception of landscape structure do coexist. This is an exceptionally simple ecosystem to empirically evaluate the interplay between spatial structure of the landscape and body size structure of local animal communities.

In this contribution, we test for the first time the connection between the body size distribution of carnivore and herbivore species in local communities and their relationship with landscape structure. We used graph theory to quantify the spatial structure of the landscape and its potential use by organisms with different dispersal abilities. For each community, we built a null model to identify the body size locations which are overrepresented (i.e. aggregations) and/or underrepresented (i.e. discontinuities) in the local communities and relate them to landscape and patch attributes.

Methods

Study site

The study site is located in the Atacama Desert, northern Chile (20°29'S, 20°26'S), which is one of the most arid ecosystems in the world (precipitation average <2 mm year⁻¹ between 1905 and 2001, Pinto et al. 2006). Here, fog-water is the main source of humidity, which is moved inland from the Pacific Ocean by the westerly winds (the prevailing wind system along the west coast of South America) (Heinz 1998). Recently, we developed a model that describes the dynamics of the vegetation biomass and of the fog-water supply, and explains the emergence of the banded vegetation pattern observed in the Atacama Desert (Borthagaray et al. 2010). In particular, the interplay between fog advection and the local topography of the system gives rise to the formation of isolated patches consisting of parallel vegetated bands of the bromeliad *Tillandsia landbeckii* (Fig. 1).

Landscape spatial structure

The landscape structure, described below, was characterized through its configuration (i.e. the spatial arrangement of the patches in the landscape) and geometry (i.e. the attributes of the patches and the vegetated bands within them) (Fig. 1).

Landscape configuration

We characterized the spatial configuration of the landscape using graph theory (Keitt et al. 1997, Urban and Keitt 2001, Economo and Keitt 2010). We used the methodology described by Keitt et al. (1997) and Urban and Keitt (2001) to identify the critical scales associated with changes in landscape connectivity, due to variations in species ability to move between patches. In this context, two patches in a network are connected by a link if the separation between them is below a critical, or threshold distance (Keitt et al. 1997). As a first approximation to identify critical scales at which landscape connectivity changes abruptly, we explored a wide range of threshold distances. Following the approach of Keitt et al. (1997) and Urban and Keitt (2001), we used several metrics to estimate landscape connectivity: 1) the number of graph components, NC, meaning clusters of nodes connected to each other but not connected through any pathway to the rest of the network, 2) the order or the number of nodes of the largest component, NO, 3) the correlation length, CL, defined as the size-weighted average connectivity of a set of clusters and 4) the landscape sensitivity, I, measured as the change in CL induced by removing each patch at different threshold distances. We also estimated the percolation point by calculating the average size of the components excluding the largest one, $\langle S \rangle^*$, as a function of the last threshold distance value removed (details of the estimation in Rozenfeld et al. 2008). The critical distance at which $< S >^*$ has a maximum is identified as the percolation point, below which a qualitative change in the connectivity state of the landscape occurs and thus the network of patches fragments into small components.

To quantify the positional importance of a vegetated patch or node in the metacommunity, three centrality metrics were measured on a minimum spanning tree (MST).



Figure 1. Aerial photograph of the study site in the Atacama Desert ($20^{\circ}29'S$, $20^{\circ}26'S$), northern Chile. (a) the spatial distribution of the 80 patches considered in the graph analysis. The dotted black line encloses the patches (n = 31) sampled to determine the local body size structure. (b) a patch to illustrate the geometry of the vegetation pattern formation. (c) a section of patch to show the parallel bands within a patch (dotted white lines).

A MST is a tree that minimizes the total length of connections between all nodes considered, maximizing the flux of individuals with different dispersal abilities among patches in the metacommunity (Urban and Keitt 2001). This approach is deemed as a useful tool to determine the relative importance of individual patches in the overall landscape connectivity (Bunn et al. 2000, Urban and Keitt 2001, Labra et al. 2005, Dale and Fortin 2010). Herein, we built the MST based on a matrix of centroid-to-centroid distances between patches and also on a matrix based on the minimum edgeto-edge distances. The centrality metrics quantified were: 1) closeness centrality, CC_i , that is, the reciprocal of the average length of the shortest path from node *i* to other nodes, 2) betweenness centrality, BC_i , which describes how often node *i* acts as a mediator on the shortest path between two nodes in the network and 3) eigenvector centrality, EC_i , defined as the first eigenvector of the adjacency matrix whose scores are proportional to the centralities of those nodes to which a target node is connected (Wasserman and Faust 1994).

Landscape geometry

We characterized the landscape geometry by attributes of the patches and the bands within them. Patch area, A (m²), and its perimeter, P (m), were estimated from an aerial photograph. In each patch, between 3 and 5 transects of 50 to 100 meters distributed perpendicularly to the bands of *T. landbeckii* were used to measure three metrics of the vegetation bands: 1) width, bw (m), 2) height, bh (m) and 3) interband distance, bd (m), defined as the linear distance between consecutive bands from the end of one band to the beginning of the following one. We also determined: 1) the vegetation dry weight, DW (kg m⁻²) from three samples of 10 cm in width that spanned perpendicularly to the band's major axis, 2) vegetation cover, C, measured as the percentage of the transect's length that is occupied by plant biomass multiplied by A, and 3) vegetation biomass B (kg) calculated as DW \times C. For each patch the mean value of bw, bh, bd, DW, C and B were estimated (indicated as bw, \overline{bh} , \overline{bd} , \overline{DW} , \overline{C} and \overline{B}) and correlated with the body size structure within the patch. We also estimated three ratios between metrics of the landscape geometry: 1) the ratio between the mean vegetation band width and the mean vegetation dry weight, $\overline{bw}/\overline{DW}$, that represents a measure of vegetation band size, accounting for variations in plant density, 2) the ratio between the mean vegetation band width and the mean vegetation interband distance, bw/bd, which refers to the regularity of the banded pattern formation, and 3) the ratio between patch area and patch perimeter, A/P, associated to the shape of the patch.

Sampling and community body-size structure data

To determine the body size structure we sampled 31 vegetated patches out of a total of 80 patches within the system (Fig. 1a, 2). Patches used in the analysis of body size patterns were chosen to cover a wide range in area, shape and connectivity between them. In large area gradients, given the same sampling effort, small patches tend to be oversampled, with collecting points close to each other, while large patches are generally undersampled, leading to poor estimates of community richness. On the other hand, a sampling effort proportional to area implies an excessive number of samples in large areas. In this context, it is desirable to have a sampling design that increases effort with sampling area but with a realistic number of samples, while ensuring confident estimations. Richness is typically linearly related to the logarithm of the total number of individuals. Assuming similar densities among patches, richness is expected to be log-linearly related to area and to the number of individuals in the patch (Wright 1983). Therefore, the sampling effort used herein was directly proportional to the logarithm (base 10) of patch area. In each patch, between 5 and 10 transects - of 50 to 150 meters - were located perpendicularly to T. landbeckii bands. Along each transect, pitfall traps of 500 cm³ were placed (between 10 and 70 pitfall traps, uniformly distributed), and checked twice during 30 days before removal. All the animals collected were preserved in 90% ethanol, identified to the finest possible taxonomic resolution by a specialist (species found listed in Table 1). The length and width of each individual caught was measured under a stereoscopic zoom microscope to estimate its biovolume, calculated as the body length \times width². All the analyses were based on a logarithmic scale (base 2). Based on published sources, each species was classified as either carnivore or herbivore.

Data analysis

We used the inverse cumulative probability distribution to assess the distribution of body sizes within communities

(Clauset et al. 2009, Newman 2005). Compared to alternative approaches based on histograms, cumulative distributions have the advantage of no loss of information due to the use of a single frequency for all the organisms within a range of body sizes (Clauset et al. 2009). Individuals from local communities were pooled together to estimate the metacommunity body size distribution. For each local community a null model was implemented to identify significant positive and negative deviations from the expected body size distribution. The essence of this null model is to determine the expected probability distribution if all the individuals observed in a local community were a random sample of the metacommunity. The expected body size distribution for each community was estimated using 2000 random samples from the metacommunity of equal size to the observed number of individuals recorded in that patch. We estimated a median and a 95% confidence interval for the expected body size distribution (null distribution) in each patch (dotted lines in the Fig. 3a). With this procedure, we have two cumulative distributions: one observed and one predicted from the null model. Possibly, one of these distributions of body sizes could present larger or smaller values than the other. However, in most cases positive and negative deviations were observed, indicating the existence of over- and underrepresentation of body sizes in local communities. These deviations are the result of ecological processes as the rates of individual arrivals and success in local communities determined by their body size, patch location and local conditions. Therefore, for each significant deviation we recorded the body size value at which this deviation was observed (Fig. 3b). Hereafter, aggregation (discontinuity) refers to the body size value at which a significant positive (negative) deviation takes place in the body size distribution of a local community. It should be highlighted that this null model is not affected by variation in the number of individuals collected in each patch.

We evaluated the existence of associations between both aggregations and discontinuities and attributes of local patches as their area, perimeter and location within the landscape and the mean values characterizing their internal geometry. A stepwise multiple regressions, selecting the best model by considering Akaike's information criterion (AIC) was used. The best model is the one with the lowest AIC (Hillborn and Mangel 1997). Differences greater than two units in AIC values between models are considered statistically significant (Richards 2005). When models with differences smaller than two units were detected, we retained the simplest one (the one with fewer parameters). We analyzed herbivorous and carnivorous species separately since the mechanisms that operate on each trophic group could be different. Within these groups, some deviations were consistently observed in different ranges of body sizes - e.g. small and large individuals. In those cases, deviations were analyzed separately.

Results

Critical scales of landscape structure

Landscape connectivity was affected by the distance threshold used to connect nodes within the network of patches.



Figure 2. Connectivity of the landscape graph as edges are sequentially removed at threshold distances of (a) 400, (b) 350, (c) 300, (d) 250, (e) 200 and (f) 100 m. Relationship between the connectivity of the landscape and the threshold distance: g) correlation length (CL), (h) average size of the components excluding the largest one, < S >* (note that the percolation point is indicated) and (i) number of components (NC) and order of the largest component (NO), (j) landscape sensitivity as a function of threshold distance and patch area in a logarithmic scale.

Table 1. The best subset of models of two variables resulted from the forward stepwise multiple regression for the herbivore (a) and carnivore (b) assemblages. All the models presented are significant, but the best one was selected following an Akaike (AIC) criterion (see the box in each case). In parenthesis () is the sign of the effect of each variable on the discontinuities or the aggregations, and its significance is indicated by an *. Abbreviations are as follows: bw: mean vegetation band width; bd: mean vegetation interband distance, bh: mean vegetation band height; DW: mean vegetation dry weight; \overline{C} : mean vegetation coberture; \overline{B} : mean vegetation biomass; A: patch area; P: patch perimeter; BC_i: betweenness centrality; CC_i: closeness centrality; EC_i: eigenvector centrality. (See the text for details on the meaning and estimation of each variable).

		Models	AIC	R ²
a) Herbivores				
Aggregation n = 21	$(\overline{bw}/\overline{DW})^2$	[+]* Log (A)	[+]* 43.43	0.54
	$(\overline{\text{bw}}/\overline{\text{DW}})$	$[+]* \log(A)$	[+]* 45.07	0.50
			[+]* 46.60	0.46
	$(\overline{DW}/\overline{DW})^2$	$[+]^{*} P$ $[+]^{*} (\overline{bw}/\overline{DW})^{2}$	$[+]^{*}$ 46.60	0.46
	$\frac{(DW/DW)^2}{(DW/)^2}$	$[+] (DW/DW)^{-}$	[-] 47.02	0.45
	$(\overline{DW}/\overline{DW})^2$	$[+]* \frac{DC_i}{Dh}$	[+] 47.05 [-] 47.95	0.43
	$(\overline{bw}/\overline{DW})^2$	$[+]^* \overline{C}$	[+] 48.20	0.42
	$(\overline{bw}/\overline{DW})$	$[+]^* \frac{C}{B}$	[+] 48.26	0.42
	$(\overline{bw}/\overline{DW})$	[+]* P	[+] 48.27	0.42
	$(\overline{bw}/\overline{DW})^2$	[+]*	48.68	0.35
Discontinuity > -3.5 (0.08 mm	³)			
n = 16	$\frac{bw^2}{c}$	[+]* bw/bd	[-] 27.31	0.62
	$\frac{bw^2}{bw^2}$	[+]* DW	[-] 27.62	0.61
	bw ²	[+]* bd	[+] 27.68	0.61
	bw ²	[+]*	27.85	0.56
	bw	$[+]^* \overline{bw/bd}$	[-] 28.17	0.60
	bw	[+]* <u>bd</u>	[+] 28.32	0.60
	bw ²	[+]* <u>bw/</u> DW	[+] 28.53	0.59
	bw	[+]* DW	[-] 28.85	0.58
Discontinuity $< -5 (0.03 \text{ mm}^3)$				
11 = 13	bd ²	[-]* bd	[+] 12.07	0.86
	\overline{bd}^2	[-]* Log (A)	[-] 19.48	0.74
	$\overline{bd^2}$	[-]*	19.88	0.69
	$\overline{bd^2}$	$[-]^* \overline{bw}$	[+] 19.88	0.74
	bd^2	[-]* B	[-] 20.60	0.72
b) Carnivores				
Aggregation > 1 (2 mm ³)				
n = 14	BCi	[+]* bw	[-]* 55.85	0.84
	BCi	[+]* <u>DW</u>	[-] 61.04	0.77
	BCi	[+]* bw/DW	[-] 61.04	0.76
	BCi	$[+]^*$	62.61	0.70
Accuration $f = \Gamma (0, 0, 2, \dots, 2)$	BCi	[+]* Log (A/P)	[+] 63.17	0.73
Aggregation $< -5 (0.03 \text{ mm}^3)$				
n = 14	Log (DW)	[-]* BC _i	[-] -3.03	0.82
	Log (A)	[-]*	5.16	0.61
	Log (A)	$[-]^*$ bd	[+] 5.88	0.64
	Log(A)	[-]* bh	[+] 6.19	0.64
	Log (DVV)	$[-]^{*} CC_{i}$	[-] 6.54	0.63
	Log (A)	$[-]^* \underbrace{CC_i}_{i}$	[-] 6.73	0.62
	Log (A)	$\begin{bmatrix} - \end{bmatrix} = \begin{bmatrix} 0 \\ - \end{bmatrix} * = \begin{bmatrix} 0 \\ - \end{bmatrix}$	[+] 7.10	0.01
	$\log (\overline{D})$		[+] 7.14	0.01
	$\log\left(\frac{DW}{DW}\right)$	[]]	7 16	0.51
Discontinuity	205 (211)	L J	,	0.55
n = 14	$\overline{bw^2}$	$[-]^* (\overline{bw}/\overline{bd})^2$	[+]* 43 99	0.68
	$\frac{1}{bw^2}$	$[-]* \overline{bw/bd}$	[+] 44.80	0.66
	bw	$[-]^* (\overline{bw}/\overline{bd})^2$	[+]* 44.98	0.66
	$\overline{bw^2}$	[-]* EC:	[+] 45.37	0.65
	bw	$[-]^* \overline{bw/bd}$	[+] 45.79	0.64
	\overline{bw}^2	[-] bw	[+] 46.40	0.62
	bw	[-]* EC _i	[+] 46.43	0.62
	bw ²	[-] CC _i	[+] 46.82	0.61
	$\overline{bw^2}$	[-]* b d	[-] 46.97	0.60
	bw ²	[-]*	47.25	0.53



Figure 3. (a) example of the inverse cumulative distribution for a local community and the detection of discontinuities and aggregations. The black line is the observed body size distribution. Each grey line is the expected distribution in a random sample of individuals from the metacommunity. The dotted black line is the 95% CI. (b) significant deviations from the null distribution indicate the occurrence of aggregations or discontinuities in those body sizes. Grey squares: negative deviations, black triangles: positive deviations, black circles: non-significant deviations. Arrows correspond to the body size values used as aggregation and discontinuity for that patch.

Figure 2a-f shows the connectivity of the landscape at six threshold distances (400, 350, 300, 250, 200 and 100 m). As was expected, the overall landscape becomes more connected as the threshold distance increases (Fig. 2g). At threshold distances between 200 and 400 m a sudden shift between the disconnected and the highly connected states occurs (Fig. 2g). This is supported by the fact that the location of the percolation point was at a threshold distance of 374 m (Fig. 2h). Moreover, at 400 m nearly 80% of the patches of the landscape are connected, comprising one large component (Fig. 2i). Accordingly, the landscape sensitivity shows the larger effects within this critical range. At distances below and above the critical range, the landscape configuration sensitivity is determined mainly by the largest patches. But within the critical range the effect of patches of intermediate size seems to be of the most importance (Fig. 2j).

Effect of landscape structure on local body size structure

The Tillandsia patches harbor communities composed of nearly 55 species, mostly arthropods, one species of lizard, Phrynosaura reichei, and one species of gecko, Phyllodactyllus gerrhopygus (list of the species found in Table 1). A total of 18 727 individuals (76% herbivores and 24% carnivores) were measured and used to identify the aggregations and discontinuities in body size distributions in each of the 31 local communities sampled (Appendix 1 Table A1). In nearly all patches, significant discontinuities (n = 29) of herbivores and aggregations of carnivores (n = 28) were detected (Table 1, Appendix 1 Fig. A1). However, both discontinuities and aggregations were concentrated in two distinct regions of the body size range (Fig. 4). Accordingly, in such cases two separate analyses were conducted, one for small-sized species and a different one for large-sized ones. In Table 1 we show the best subset of models that describe the relationships between aggregations and discontinuities in the herbivore and carnivore assemblages with landscape configuration and geometry attributes. In addition, Table 2 summarizes the main results of the herbivores' and carnivores' structure in a qualitative manner.

Herbivores' structure

The distribution of herbivores body size (expressed as biovolume) ranges in a logarithmic scale from -8 (~0.004 mm³) to 5.5 (~45 mm³). However, we found significant aggregations and discontinuities only below a biovolume of 1 (~2 mm³), and therefore there were not significant deviations for herbivores larger than 1 mm³ (Fig. 4a).

In the herbivore assemblages (n = 14 312 individuals), the body size structure was associated with internal attributes of the patches such as mean vegetation band width (\overline{bw}) , mean vegetation interband distance (\overline{bd}) , patch area (A) and mean vegetation dry weight (\overline{DW}) (Table 1, Fig. 5). None of the metrics associated with the centrality of the patches in the landscape were selected by the best subset of models to explain the herbivores' structure (Table 1). Our results show that the location of discontinuities $>0.08 \text{ mm}^3$ (~ -3.5 in a logarithmic scale) is an increasing non-linear function of the mean vegetation band width (bw, Fig. 5a), while the location of discontinuities $< 0.03 \text{ mm}^3$ (~ -5 in a logarithmic scale) is a decreasing non-linear function of mean vegetation interband distance (bd, Fig. 5b). It should be noted that we did not find significant discontinuities between -3.5 and -5 for herbivore species.

Aggregations were mainly related to the ratio between mean vegetation band width and mean vegetation dry weight $(\overline{bw}/\overline{DW}, Fig. 5c)$. In addition, patch area (A) was also positively related to the location of aggregations (Table 1). In this last case, we selected two models by the AIC rank, differing in the inclusion of $\overline{bw}/\overline{DW}$ as either a linear or a quadratic term.

Carnivores' structure

The distribution of carnivores' body size (expressed as biovolume) ranged in logarithmic scale from -10 (~0.001 mm³) to 12 (~4.096 mm³). Significant aggregations and discontinuities were found for the smaller sized individuals (< -5 Table 2. Summary of the main results of the effects of patch and landscape attributes on body size structure of the herbivore and carnivore assemblages. The \uparrow (\downarrow) indicates that when a patch or landscape attribute increases the body size value at which the aggregation or discontinuity occur in the body size distribution increases (decreases). Patch attributes: \overline{bw} : mean vegetation band width, \overline{bd} : mean vegetation interband distance and $\overline{bw/DW}$: mean vegetation band width standardized by the dry weight. Landscape attribute: BC;: betweenness centrality.

		Patch		Landscape	
		bw	\overline{bd}	bw/DW	BC _i
Herbivores	Small-size discontinuity Large-size discontinuity Large-size aggregation	\downarrow	\uparrow	¢	
Carnivores	Small-size discontinuity Small-size aggregation Large-size aggregation	\downarrow			$\stackrel{\downarrow}{\uparrow}$

in a logarithmic scale or 0.03 mm^3) and for the larger ones (> 0 in a logarithmic scale or 1 mm³) (Fig. 4b). In agreement with previous results, we did not find significant deviations for species of carnivores ranging in size between 0 and -5 (in a logarithmic scale).

In the carnivore species assemblages (n = 4415), aggregations and discontinuities in body size distributions were related to patch geometry, but in the case of aggregations, they were also related to landscape configuration (Table 1, Fig. 6). The discontinuities of small-sized carnivores (< 0.03mm³) were associated with band attributes, showing a negative non-linear relationship with mean vegetation band width (bw, Fig. 6a). In addition, the ratio between mean vegetation band width and mean vegetation interband distance (bw/bd) was negatively associated with the location of discontinuities in body size. In this case, the models with the lowest AIC, but with less than two AIC units of difference, involved the same variables expressed both in linear and quadratic formulations (Table 1).

Carnivores' aggregations were associated with betweenness centrality BC_i (based on a matrix with the minimum edge to edge distances), mean vegetation band width ($\overline{\rm bw}$) and mean vegetation dry weight ($\overline{\rm DW}$). However, it should be highlighted that we did not find significant size aggregations between 0 to -5 in logarithmic scale (0.03–1 mm³) for carnivores. As a result of that, two separate analyses below and above this range were did it. In the case of small-size aggregations (< 0.03 mm³) the relationship with BC_i was linear and negative (Fig. 6b), while the opposite tendency was observed for aggregations >1 mm³ (Fig. 6c). Interestingly, both mean vegetation band width (bw) and mean vegetation dry weight ($\overline{\rm DW}$) were associated with the location of carnivore body size aggregations.

Discussion

The approach carried out in this study allowed for the detection of significant discontinuities and aggregations in the body size distributions of local communities in the Atacama Desert. The body sizes at which these discontinuities and aggregations were observed in each community were related to properties of the patch network (i.e. configuration), such as connectivity, and with local patch attributes (i.e. geometry) such as area and banding pattern. Several conceptual frameworks emphasize the role of landscape structure in the organization and composition of biological communities (MacArthur and Wilson 1967, Holling 1992, Hanski 1999, Hubbell 2001, Holyoak et al. 2005, Ritchie 2010). However, as far as we know, few studies have previously shown empirical evidence of a relationship between landscape structure and body size distributions (Brown 1995, Gaston and Blackburn 2000, Etienne and Olff 2004).

Species in the Atacama Desert metacommunity probably perceive the environment as fragmented or as continuous depending on their body size. Indeed, we identified a critical range between 200 and 400 m at which an abrupt change from discrete habitat patches to a highly connected landscape occurs (Fig. 2). This abrupt change in the landscape perception is associated with large increases in resource availability for those animals that can move above the percolation threshold



Figure 4. Location of body size values at which significant positive (aggregations) and negative (discontinuities) deviations were found among all the local communities for herbivore (a) and carnivore (b) assemblages.



Figure 5. Effect of patch attributes on the body size structure of the herbivore assemblages. (a–b) location of discontinuities in the body size distributions of local communities in relation to mean vegetation band width and vegetation interband distance. (C) location of aggregations in the body size distributions as a function of the mean vegetation band width standardized by its dry weight. Only the first variable included in each model are presented (Table 1a).

(Kolasa 1989, Peterson et al. 1998, Olff and Ritchie 2002, Szabó and Meszén 2006). Consequently, animals with a vagility either above or below this threshold value should effectively experience contrasting landscapes regarding habitat and resource availability. In the communities presently studied, body sizes of individuals vary across a range of nearly four orders of magnitude. Undoubtedly, the scale of movement of the large-sized individuals (e.g. lizards, geckos) and small ones (e.g. mites, booklice, beetles; but see below) should be above and below the threshold value for landscape perceptions, respectively (Tsagkarakou 1999, Ranius and Hedin 2001, Hoehn et al. 2007). This implies a large, and probably abrupt, change in the total amount of resources that different organisms can access in the same metacommunity. The existence of migration between patches has been suggested as a requisite for the persistence of large carnivore species (McCann et al. 2005, Arim et al. 2010). It should be noted that most of the larger body-size individuals in the studied system correspond to carnivore species. Accordingly, the patterns of occurrence of discontinuities and aggregations in the body size distributions of carnivores and herbivores assemblages could reflect their differential movement ability and energetic demands. We found that in the case of the herbivores' size structure, both discontinuities and aggregations are better explained by the internal attributes of patches (Fig. 5). However, the carnivores' body size structure was more sensitive to the spatial arrangement of patches in the landscape (Fig. 6). This represents a qualitative change in the nature



Figure 6. Effect of landscape configuration and patch attributes on the body size structure of the carnivore assemblages. (a) location of discontinuities in the body size distributions of local communities in relation to the mean vegetation band width. (b–c) location of aggregations in the body size distributions as a function of the betweenness centrality of each patch. Each case corresponds to the first variable included in the model, except in case (b) (Table 1b).

and scale of the limiting factors controlling size distribution within each trophic group.

The location of aggregations in the carnivore assemblage is affected by the connectivity of the habitat patches. Interestingly, this tendency is negative for small animals (< 0.03mm³), while positive for larger ones ($> 2 \text{ mm}^3$). Further, intermediate size classes did not present significant aggregations in any of the local communities. This last pattern could be associated with the compromise between resource acquisition and its transformation into offspring, which allows species of intermediate body size to satisfy their requirement with a minimum of resources (Marquet and Taper 1998). Medium-sized individuals should be less sensitive to landscape fragmentation and therefore, to an isolation effect. This is supported by the fact that intermediate size classes did not significantly deviate from the null model, while significant aggregations were observed at larger or smaller size values. Both aggregations move to more extreme values of body size as the connectivity of the patch increases. This pattern could be accounted for by the active and passive dispersion of individuals and the probability of finding a new patch in the landscape. Large sized animals have high dispersal capability (Peters 1983), but this general allometric pattern could revert in the smaller individuals, for which passive dispersal could be important in the study system. Wind is a dominant force in the Atacama Desert, moving a large amount of sand particles. The smallest body sizes in the metacommunity are comparable to the diameter of a sand particle (0.0625 to 2 mm) and could be easily moved by the blowing wind. The colonization of a suitable patch after being dispersed either by wind or active transportation is probably affected by patch connectivity, explaining the tendency of aggregations to be located at extreme size values when connectivity is higher.

One important feature in the Atacama Desert ecosystem is the presence of only one species of plant responsible of the banded pattern formation (Borthagaray et al. 2010). This allowed us to evaluate the effect of the geometry of the vegetation bands on the herbivores' body size distributions, ruling out the potential effect of an increase in the diversity of the vegetation assemblage (Morse et al. 1985, Gunnarsson 1992, Siemann et al. 1998, Jonsson et al. 2009). Herein, we reported a positive relationship between the location of the aggregations of the larger herbivores and the mean vegetation band width standardized by the biomass. This represents a measure of band size, which accounts for variations in the density of plants. Notably, the location of discontinuities for larger herbivores was congruent with the location of their aggregations, such that when both deviations were detected in a community, discontinuities were located closer but at larger body size values than did aggregations ($t_{14} = -9.1$; p < 0.0001). This implies the existence of a congruent variation among communities where body sizes tend to accumulate previous to a discontinuity. Further, the location of both discontinuities and aggregations of herbivores increase together in association with the mean vegetation band width (Fig. 5a, c), pointing to a joint interpretation of these variations. In this sense, the observed results suggest the existence of a positive association between the size of local bands and the body size of the larger herbivores inhabiting the patch, a pattern previously observed among large landmasses but not at smaller scales (Marquet and Taper 1998, Burness et al. 2001). Finally and consistently, the location of discontinuities identified in the smaller carnivores' and herbivores' assemblages were associated with the mean vegetation band width and the mean interband distance, respectively. Both patterns represent spatial restrictions imposed by the band geometry on small body size individuals, supporting a main role for the internal banding structure in affecting the viability of small size individuals.

The interplay between landscape structure and body size distributions seems to be of great importance for understanding how local communities are assembled in nature. In this study, we recognize a putative role of landscape configuration (i.e. metacommunity network), as well as local patch geometry on community structure. We suggest that discontinuities and aggregations are likely determined by restrictions and advantages related to the size of individuals. Several mechanisms could account for the viability of large body sized species (Burness et al. 2001, Carbone et al. 2007). However, determinants of smaller size viability and abundance have received less attention both in empirical and theoretical studies (Marquet and Taper 1998). We suggest that the body size structure observed in local communities reflects landscape structure, a pattern which has received relatively little attention in the literature. We hope that this study contributes to advance our understanding of landscape determinants of community structure and motivates further studies oriented toward this aim.

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Appendix 1



Figure A1. Spatial distribution of the discontinuities and the aggregations on a minimum spanning tree (MST) based on a matrix of the minimum edge-to-edge distances. The dotted black line encloses the 31 patches sampled and on each of those patches is indicated if a significant discontinuity or aggregation occurs (filled black circle). (a) herbivores: the left panel shows the discontinuity while the right panel shows the aggregations. (b) carnivores: the left panel shows the discontinuity while the right panel shows the aggregations.

Table A1. List of the species found it in the Atacama Desert, northern Chile. Mean biovolume (mm³) and its standard deviation ($\overline{X} \pm SD$) are presented for each species. *Acariformes correspond to a superorder. All cases indicated as sp. refer to a morphospecies. Species without SD are cases represented by only one individual in all the system.

Order	Family	Genus/Species	Common name	\overline{X}	SD
Acariformes*		sp.1	mite	0,017	± 0,0068
Acariformes*		sp.2	mite	0,028	± 0,0220
Acariformes*		sp.3	mite	0,042	± 0,0114
Acariformes*		sp.4	mite	0,420	± 0,2089
Acariformes*		sp.5	mite	0,214	± 0,1915
Araneida	Anyphaenidae			8,673	± 3,6350
Araneida	Lycosidae		wolf spider	63,127	$\pm 44,4661$
Araneida	Óonopidae	Unicorn sp.	goblin spider	10,239	$\pm 10,6836$
Araneida	Oonopidae	·	goblin spider	0,132	± 0,0091
Araneida	Salticidae	Thiodina nicoleti	jumping spider	1,730	\pm 0,9509
Araneida	Salticidae		jumping spider	2,075	± 1,2923
Araneida	Sicariidae	Sicarius sp.1	assassin spiders	106,50	± 48,6
Araneida	Sicariidae	Sicarius sp.2	assassin spiders	2,001	± 2,0821
Araneida	Zodariidae	Platnickia sp.	ground or ant spider	14,098	± 9,9623
Araneida		sp.1	0 1	0,543	± 0,0607
Araneida		sp.2		1,256	± 0.5633
Araneida		sp.3		0.412	± 0.5336
Araneida		sp.4		0.430	+ 0.1820
Araneida		sp. 5		0.154	_ 0/1020
Coleoptera	Anobiidae	Acustotheca sp.	beetle	4.586	+ 1.5415
Coleoptera	Dytiscidae	· · · · · · · · · · · · · · · · · · ·		0 588	+ 0.4314
Coleoptera	Nitidulidae	sn 1	san beetles	20.874	_ 0,1511
Coleoptera	Nitidulidae	sp.2	sap beetles	3.011	_
Coleoptera	Tenebrionidae	Philorea aracniformes	sup seeries	287.38	_
Coleoptera	Tenebrionidae	Philorea maritima		28.125	_
Coleoptera	Tenebrionidae	Physogaster sp.		21,977	± 8.9112
Coleoptera	Tenebrionidae	sp.1		224.13	+ 199.1
Coleoptera	Tenebrionidae	sp.2		20.741	+ 4.9133
Coleoptera	Tenebrionidae	sp.2		35,881	+ 6.6274
Coleoptera	Tenebrionidae	sp.4		6.828	
Diptera	Mycetophilidae	SP		1,134	_
Diptera	Otitidae	sp.1	picture-winged fly	1.246	_
Diptera	Otitidae	sp.2	picture-winged fly	1,246	± 0,8637
Diptera	Sarcophagidae		1 0 /	3,186	,
Diptera	Scatopsidae			0,309	± 0,0756
Diptera	Sciaridae			0,029	± 0,0000
Diptera	Tephritidae			1,134	,
Diptera	Trephriridae	Trupanea sp.	fruit flies	0.645	± 0.2731
Hemiptera	Hebridae	, ,	velvet water bugs	0,123	,
Homoptera	Cicadellidae		0	0,360	_
Hymenoptera	Formicidae	Dorymyrmex sp.	ant	2,833	± 1,9326
Hymenoptera	Mymaridae	/ / 1		0,011	± 0,0134
Hymenoptera	Pteromalidae			0,142	± 0,0771
Lepidoptera	Gelechiidae			0,781	_
Lepidoptera	Noctuidae	Syngrapha gammoides	owlet moths	272,00	_
Lepidoptera	Sphingidae	Protoparce sexta	moths	3000,00	_
Lepidoptera	Tineidae	,	tineid moths	0,781	-
Pseudoscorpi- onida	Chernetidae		pseudoscorpion	0,878	± 0,7658
Psocoptera	Liposcelidae		booklice	0,184	± 0,0890
Scorpionidea	Bothriuridae	Brachistosternus	scorpion	2126,82	± 1190,8
Califurna	A	matoni	aug antida ::	15.000	
Solifugae	Ammotrechidae	<i>Mummucia</i> sp.	sun spiders	15,869	$\pm 35,7042$
Sollitugae	Ammotrechidae	Dhulla da stala	sun spiaers	10,651	$\pm 10,5/85$
Squamata	Секкопіdae	Phyliodactylus gerrhopygus	деско	1408,98	± /95,9
Squamata	Tropiduridae	Phrynosaura reichei	lizard	2306,46	± 1510,9
Thysanura	Lepismatidae	<i>Lepisma</i> sp.	silverfish	3,299	± 1,9898
Thysanura	Maindroniidae	<i>Maindronia</i> sp.		10,186	± 13,1631
Trichoptera				0,370	± 0,0550