Journal of Vegetation Science 18: 911-920, 2007
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Filtering processes in the assembly of plant communities: Are species presence and abundance driven by the same traits?

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Abstract

Question: Is the response of plant traits to environment at the community level similar when considering species abundance and when considering species presence only?

Location: Mountain grasslands, central Argentina.

Methods: We used data from 57 floristic samples, ordinated through DCCA along moisture and grazing gradients combined with trait values from 85 species (plant height, leaf area, leaf thickness leaf toughness and SLA). For each sample, we calculated the weighted average (considering species abundance) and the simple average (considering only species presence). Through multiple regressions we analysed how each average (dependent variable) responded to moisture and grazing (DCCA scores along Axes 1 and 2, respectively, as independent variables).

Results: Weighted averages of all traits were significantly associated to both gradients, while simple averages did not always respond. In some cases the responses followed similar but weaker trends than the responses of weighted averages, but in other cases these responses were qualitatively different. Traits more associated with size (plant height, leaf area, leaf thickness) responded more consistently (similar trends for both averages) to grazing than to moisture, while traits more associated with plant resource acquisition (SLA, leaf toughness) responded more consistently to moisture than to grazing.

Conclusion: The trait values and combinations which determine the probability of species presence are not necessary the same as those which determine their probability of becoming abundant. To understand community assembly rules, both species presence and species abundance should be taken into account as the result of different, although closely linked, filtering processes.

Keywords: Argentina; Assembly rule; Central Argentina; Community structure; Dominant; Filter; Gradient analysis; Grassland; Plant trait.

Abbreviation: SLA = Specific leaf area.

Introduction

It is well known that plant community composition varies across local and regional environmental gradients (Whittaker 1956). The mechanism by which plant assemblages respond to environmental factors can be viewed as a process of species deletion where the biotic and abiotic environment acts as a filter for the regional species pool, removing those species (or, more realistically, increasing their probability of being removed) lacking the adequate trait attributes for persisting under that given set of conditions (Keddy 1992; Díaz et al. 1998). However, not all species which persist in a community attain the same abundance. In general, plant communities have a typical structure with a relatively small number of dominant species which account for a high proportion of the total biomass, and a large number of minor species that account for a low proportion of the biomass (Whittaker 1965; Grime 1998). Considering this, and given a regional pool of species, a plant assemblage can be viewed as the result of two filtering processes. A first-level filtering process, that determines which species (according to their particular combinations of trait values) have more probability to be present under certain conditions and a second-level filtering process, that determines which of the species present have more probability of becoming dominant (Keddy 1992). Although in nature both filters probably act simultaneously, the conceptual differentiation between them could be important in understanding how communities are assembled under varying environmental conditions.

In order to understand plant responses to environment, different authors have analysed the relationship between plant attributes with variables such as insolation (Ackerly et al. 2002), time from cultivation abandonment (Garnier et al. 2004), grazing (Díaz et al. 2001; Cingolani et al. 2005a), fire (Gurvich et al. 2005), soil nutrient status (Grime 1974), precipitation (Díaz et al. 1998) or a combination of these and other factors (Díaz et al. 1999; Fonseca et al. 2000; De Bello et al. 2005; Garnier et al. 2006; Gross et al. 2007). These analyses have been performed at either the species or the community level. In the first case, a set of species is selected with varying criteria (e.g. only dominants, dominants plus most frequent subordinates, a random sample, all species) and responses to the environmental factor under study is related with one or more plant characteristics (e.g. Díaz et al. 2001). At the community level, sites under different environmental conditions are selected, and for each site a mean value for each trait (in the case of continuous traits) is calculated from the values of component species. This value can be calculated, giving to each species a similar weight (simple average, e.g. Fonseca et al. 2000) or weighting each species by its relative abundance at the site (weighted average, e.g. Louault et al. 2005; Garnier et al. 2006).

These different ways of analysing trait-environment relationships do not always lead to similar results. In some cases, unexpected contrasting patterns emerged with the different approaches. For example, Ackerly et al. (2002), considering all woody species, obtained far stronger responses of plant traits to insolation when using weighted averages, than when using simple averages or when performing a species level analysis. Garnier et al. (2004), when analysing data at the species level along a successional gradient, obtained stronger relationships when only dominant species were considered, than when all species were included. Cingolani et al. (2005a), using data from various abundant and minor species, obtained different and more clear patterns of plant traits responses to grazing at the community level (using weighted averages) than at the species level.

These antecedents suggest that, in a given plant assemblage, dominants should have trait values better fitted to environment than minor species. Thus, as more importance is given to minor species in the analyses (either by including a higher number of them in the species level analysis or by assigning them the same weight as dominants in the community level analysis), the less clear and weaker will the trait-environment relationships appear. This would mean that the first-level filter (which determines species presence-absence probabilities) is weaker than the second-level filter (which determines species probability of becoming dominant). We aimed to test this hypothesis using five plant traits and two local gradients of moisture and grazing. Our approach was to analyse data at the community level, comparing the response of simple averages with the response of weighted averages to the combination of both gradients. The response of simple averages can be interpreted as the result of the first-level filter only, while the response of weighted averages can be interpreted as the final result of the two filtering levels acting together. Specifically, we aimed to (1) analyse the response of weighted and simple trait value averages to local gradients of moisture and grazing and (2) analyse the differences between both response curves along the environmental gradients. We predict that responses of simple averages will show similar trends, but with weaker slopes, than the response of weighted averages, being the difference between both curves not constant along the gradients.

Material and Methods

Study area

The study was carried out in Pampa de Achala (31° 34' S, 64° 50' W), a dissected plateau located between 1800 and 2300 m a.s.l. in the Córdoba mountains, central Argentina. Mean temperatures of the coldest and warmest months are 5 ºC and 11.4 ºC, respectively, and there is no frost-free month. Annual rainfall is 950 mm, concentrated between October and April (Cabido 1985; Colladon 2000). The landscape consists of a mosaic of grasslands, *Polylepis australis* woodlands, granite outcrops and eroded areas with exposed rock surfaces (Cingolani et al. 2004). The study was carried out in grassland communities, which have a productivity of ca. 450 and 750g.m^{-2}.a^{-1} when grazed and excluded from grazing, respectively (Pucheta et al. 1998). The main land use is livestock raising (mainly cattle), which began early in the 17th century and completely replaced large native herbivores by the beginning of the 20th century (Díaz et al. 1994).

Soil moisture and grazing gradients

We based the present study on data and results from Cingolani et al. (2003), combined with measurements on plant traits obtained from Díaz et al. (2004). In the previous article (Cingolani et al. 2003), we described two main gradients of species composition for the study area on the basis of 57 floristic samples (36 m^2 each), where cover of all vascular plants was estimated using the Braun-Blanquet scale. Using Detrended Canonical Correspondence Analysis (DCCA, ter Braak 1987), we related those gradients to topography and soil characteristics on the one hand (DCCA Axis 1), and to past and present grazing intensity (DCCA Axis 2) on the other. In this way, the 57 samples used for the analyses were positioned along DCCA axes 1 and 2 according to linear combinations of their abiotic characteristics and grazing indicators respectively (Fig. 1). Axis 1 represents a moisture availability gradient, and its arbitrary subdivision allowed us to distinguish three main habitat types: xeric

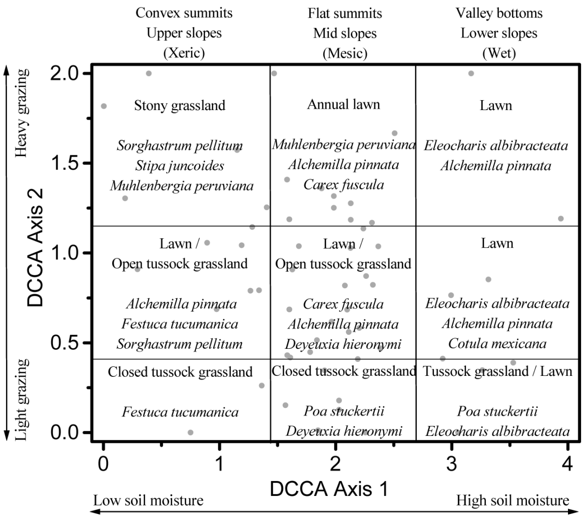

Fig. 1. Ordination of samples (grey points) along DCCA Axis 1 and DCCA Axis 2 (rescaled), representing grazing and moisture respectively. For each sector of the ordination plot, vegetation physiognomy together with dominant and some characteristic species are indicated (adapted from Cingolani et al. 2003).

habitats at upper topographic positions, mesic habitats at intermediate topographic positions and wet habitats at low and flooded topographic positions (Cingolani et al. 2003). Ungrazed communities in the xeric, mesic and wet sectors of the gradient all have high standing biomass and productivity, which are positively interrelated, throughout the whole year (Pucheta et al. 1998; 2004). However, in the dry season (winter and early spring) the xeric habitat is the harshest to plants due to water scarcity, while in the rainy season the most restricting conditions appear in the wettest end of the gradient, due to waterlogging (Cingolani et al. 2003).

Axis 2 represents a grazing gradient, obtained by the combination of past and present grazing indicators such as dung deposition, soil impedance and evidences of livestock induced soil erosion. To better reflect the grazing gradient, in the present study DCCA Axis 2 was rescaled so that samples in the three segments (habitat types) varied from 0 (in all cases corresponding to long-term exclosures on well preserved soils) to 2 (in all cases corresponding to sites in heavily stocked paddocks, with high present grazing intensity and evidences of heavy grazing in the past). This rescaled axis (Fig. 1) is highly correlated with the original DCCA Axis 2 ($R = 0.94$, $P < 0.001$; Pearson correlation coefficient) and is better correlated than the original DCCA Axis 2 to each individual grazing indicator. Additionally, ancillary information on stocking rates for some of the sites confirmed that the rescaled Axis 2 was a better surrogate of time integrated stocking rates across the whole moisture gradient than the original Axis 2. The subdivision between habitat types was used in this study only for this rescaling, but was not considered for the statistical analyses (see below). Turnover of floristic composition along the moisture gradient is almost complete, and only partial along the grazing gradient (Cingolani et al. 2003).

Plant traits measurements

We considered the following plant traits: leaf toughness (measured as leaf tensile strength, *N*/mm), leaf area (mm^2), specific leaf area (SLA; mm^2.mg^{-1}), leaf thickness (mm) and plant height (cm). These traits are the most important in defining the general syndromes of plant resource capture, storage and release identified by Díaz et al. (2004). They are also fundamental in the definition of plant general strategy (Grime et al. 1997; Westoby 1998) and response to grazing (Díaz et al. 2001, 2007; Cingolani et al. 2005a). Trait values were obtained from the Córdoba Ecological Database (Díaz et al. 2004 and unpubl. data) for 85 species (most of them grasses and forbs) present in the 57 floristic samples. Each species was present in a minimum of one sample (seven species) to a maximum of 54 samples (one species), with a mean of 15 samples. Plant traits were measured following the procedures of Cornelissen et al. (2003). Dominants and most minor species were included in the species dataset, representing between 78% and 100% of the relative vegetation cover of the samples, with a mean of 96%, which is in accordance to the sample protocol suggested by Pakeman & Quested (2007). In terms of number of species, our dataset represented between 68% and 100% of the total number of species present in any given sample, with a mean of 85%. Although species have internal variability in their trait values, the method of choosing a unique (mean) value for each species is widely used, based on the assumption that within-species variability is lower than between-species variability (Díaz & Cabido 1997; Westoby 1998; Cornelissen et al. 2003; Garnier et al. 2004). In this way, our method only detects plant trait shifts owing to species replacement, and misses shifts caused by internal variability within species.

Data analyses

For each of the 57 samples we calculated the weighted and the simple averages for each trait. Before averaging, we transformed the Braun-Blanquet scale of abundance into cover values representing the central class point (Kent & Coker 1992) and then ln transformed all traits, except SLA, to meet normality and obtain averages better representative of the central tendencies. For the case of leaf toughness and leaf thickness, previous to the transformation we multiplied their values by ten to avoid negative values. In these calculations, the simple average represents the most probable trait value (or more exactly the central point of the most probable interval of values) which would be obtained if selecting a species of the community at random. The weighted average in turn represents the most probable value which would be obtained if we select a point of space at random and measured the species present in it. For the same sample, a large difference between both averages would indicate more extreme trait values of dominants in relation to the majority of the species. A similar value would mean that dominants are not different from the majority of species, or that all species are present in similar abundance. In our dataset, all samples have a typical dominance diversity curve with few dominants and a high number of minor species, although dominance is stronger in less grazed sites (Cingolani et al. 2003).

We analysed the response of each plant trait to the moisture and grazing gradients through multiple regressions. For each trait, two different regressions were performed, with the weighted and the simple average as the dependent variables. The independent variables were the sample scores in DCCA Axes 1 and 2. We also considered quadratic and square-root terms to detect nonlinear relations. For each analysis, we first selected the best combination of variables and terms by backward stepwise regression, with $P \leq 0.1$ for removal and a $P \leq 0.05$ for entry (Afifi & Clark 1984), but if the three terms of the same variable (quadratic, square-root and first-order) were selected by the automatic procedure, we manually discarded one of them (maintaining the significant one or two terms which produce the highest r^2), to avoid biologically meaningless relationships (we only allowed for monotonic, unimodal or U-shaped relationships). In a second selection step, if both DCCA axes were selected in the model, we checked for interactions between them by including in the regression all the possible products of the selected terms involving both axes. We selected significant interactions by a manual procedure. Once the final model was selected, we checked for normality of residuals through Kolmogorov-Smirnov tests.

Differences between weighted and simple averages at different combinations of environmental conditions (moisture and grazing) were analysed from the confidence intervals of the response curves. To perform this comparison, we calculated from the regression equations the predicted mean values and their confidence intervals at 289 different combinations of grazing and moisture. This value was decided arbitrarily by selecting points at intervals of 0.25 for Axis 1 and of 0.125 for Axis 2 (17 values in each case). Larger intervals produced more blurred patterns and shorter intervals proved not to be necessary. From these data, points were classified in three classes: (1) cases where weighted average did not significantly differ from simple average, (2) cases where weighted average was higher than simple average and (3) cases where weighted average was lower than simple average. Points were displayed in a two-dimensional plot of DCCA Axis 1 vs 2, and from that plot we delimited the areas corresponding to each class.

Table 1. Variance explained by each DCCA axis for the simple and weighted averages of each trait, by the interaction between axes, and total variance explained by the model. The sign (+ or -) indicates the general trend in the case of monotonic relationships, and the ∩ and ∪ symbols indicate non-monotonic relationships. See Table 2 for complete formulae.

		DCCA Axis 1 (moisture)		DCCA Axis 2 (grazing)		Interaction	Total	P_{model}
Plant height (cm)	Weighted	3.0	-	60.4	-	ns	63.4	< 0.0001
	Simple	ns		41.6	-	ns	41.6	< 0.0001
Leaf area (mm^2)	Weighted	14.8	∩	32.4	-	ns	47.2	< 0.0001
	Simple	41.4	+	27.1	-	ns	68.5	< 0.0001
Leaf thickness (mm)	Weighted	16.2	∪	24.1	-	ns	40.3	< 0.0001
	Simple	ns		8.6	-	ns	8.6	0.0270
Leaf toughness (N mm-1)	Weighted	15.9	-	40.1	-	ns	56.0	< 0.0001
	Simple	23.9	-	7.8	+	ns	31.7	< 0.0001
SLA (mm^2 mg^{-1})	Weighted	40.4	+/=	15.5	+/∩	13.2	69.1	< 0.0001
	Simple	68.1	+	ns		ns	68.1	< 0.0001

ns : not significant, + : positive relationship, - : negative relationship, ∩ : unimodal relationship; ∪: u-shaped relationship, = : no relationship. In cases of interaction, more than one symbol indicates the different trends of the relation according to the values of the other variable (see Fig. 3).

Results

General patterns

For all traits, variation of each average in function of DCCA Axis 1 (moisture) and DCCA Axis 2 (grazing) is shown in Fig. 2. To show the trait variation with moisture we considered grazing as a constant (moderate) value, and to show trait variation with grazing we considered moisture as a constant (moderate) value. For most cases the shape and slopes of the curves would be the same if considering higher or lower constant values, with the only exception being SLA weighted average, where interactions were detected (Table 1, Fig. 3).

We found different results for weighted than for simple averages. While weighted averages were responsive to both gradients in all cases, simple averages were not and, when responding, responses were weaker (less pronounced slopes) or similar, but never stronger (Fig. 2a, b), than the responses of weighted averages, and in some cases even followed a different trend. Additionally, variance explained by environmental gradients was in general higher for weighted than for simple averages (Table 1). The comparisons of the predicted values through their confidence intervals indicate that differences between both averages were not constant along the gradients, and in some cases were inverted, meaning that, depending on environmental conditions, dominants can have higher, similar or lower trait values than the majority of species (Fig. 2c).

Variation of single traits

Plant height responded to moisture differently for weighted than for simple average. While the weighted average decreased with moisture, the simple average did not vary (Fig. 2a). Response to grazing, in turn, was qualitatively similar for both averages, plants becoming shorter as grazing increased. However, the response of the weighted average was far stronger (i.e. the slope of the relationship was steeper) than the response of the simple average (Fig. 2b). With low moisture and no/light grazing, the weighted average was significantly higher than the simple average, indicating that dominants were among the tallest species present in the community. As grazing and/or moisture increased, differences were progressively smaller until they became non-significant. Finally, at wet sites with heavy grazing, the differences were inverted, and simple averages became higher than weighted averages, indicating that dominants were among the shortest species present in the community (Fig. 2c).

Leaf area also responded to moisture differently according to which average was considered. The weighted average showed a unimodal response to moisture while the simple average showed a positive response, indicating that species with large leaves were proportionally more numerous at wet sites than in other parts of the gradient, but proportionally more abundant at mesic sites (Fig. 2a). The response to grazing was, in turn, qualitatively similar for both averages, indicating a decrease of leaf area with increasing grazing (Fig. 2b). In most situations, the two averages did not differ, except in wet sites with heavy grazing, where simple averages were greater than weighted averages, and in mesic sites with light grazing, where weighted averages were greater than simple averages (Fig. 2c).

Leaf thickness showed a U-shaped response to moisture in the case of weighted average and no response in the case of simple average (Fig. 2a). The response to grazing was negative for both averages, but stronger in the case of the weighted average (Fig. 2b). In mesic sites, except those with very light/no grazing, simple averages were significantly higher than weighted averages, indicating that dominants had thin leaves compared with the majority of the species. Under heavy grazing, this difference was extended to more xeric and to wetter

Table 2. Full models obtained by stepwise regression procedures for weighted and simple averages of the five traits under study in function of DCCA Axis 1 (moisture) and DCCA Axis 2 (grazing).

Weighted averages

$\mathrm{Ln}\ (\text{Plant height}) = 4.461 - 0.048\ (\text{Axis\_1})^2 - 2.040\ (\text{Axis\_2})^{1/2}$
$\mathrm{Ln}\ (\text{Leaf area}) = 5.512 + 0.908\ (\text{Axis\_1}) - 0.181\ (\text{Axis\_1})^2$
$\mathrm{Ln}\ (10\ \text{Leaf thickness}) = 1.607 + 0.398 - (\text{Axis\_1}) - 0.863\ (\text{Axis\_1})^{1/2} - 0.221\ (\text{Axis\_2})2$
$\mathrm{Ln}\ (10\ \text{Leaf toughness}) = 4.726 - 0.081\ (\text{Axis\_1})^2 - 1.641\ (\text{Axis\_2}) + 0.448\ (\text{Axis\_2})^2$
$\mathrm{SLA} = 6.133 + 0.622\ (\text{Axis\_1}) + 5.785\ (\text{Axis\_2}) - 2.011\ (\text{Axis\_2})^{1/2} + 1.979\ (\text{Axis\_1})^2 \times (\text{Axis\_2})^{1/2} - 1.796\ (\text{Axis\_1})^2 \times (\text{Axis\_2})$

Simple averages

$\mathrm{Ln}\ (\text{Plant height}) = 2.447 - 0.367\ (\text{Axis\_2})^{1/2}$
$\mathrm{Ln}\ (\text{Leaf area}) = 4.828 + 0.307\ (\text{Axis\_1})$
$\mathrm{Ln}\ (10\ \text{Leaf thickness}) = 1.253 - 0.060\ (\text{Axis\_2})^{1/2}$
$\mathrm{Ln}\ (10\ \text{Leaf toughness}) = 3.165 - 0.182\ (\text{Axis\_1})^{1/2} + 0.124\ (\text{Axis\_2})^{1/2}$
$\mathrm{SLA} = 12.795 + 0.466\ (\text{Axis\_1})^2$

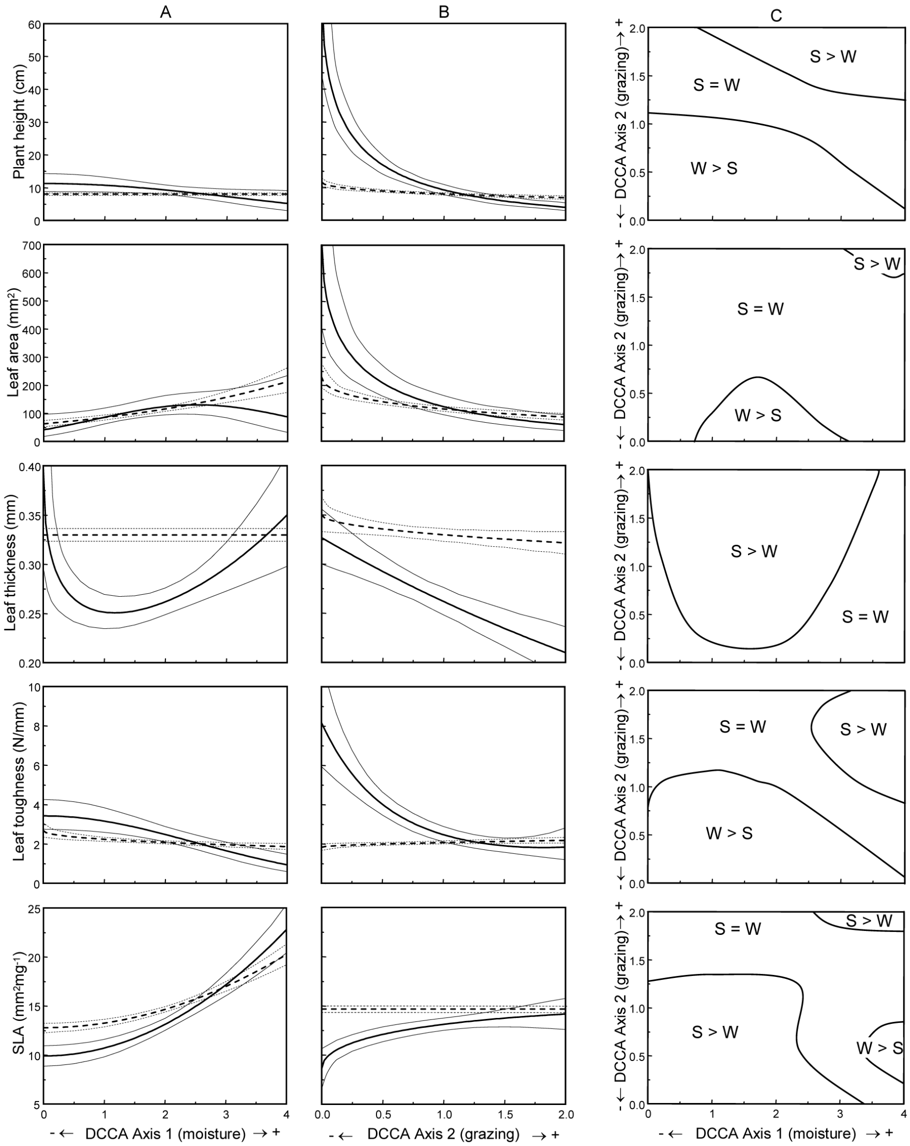

Fig. 2. **A**. Variation of simple (- - - -) and weighted (——) averages of all plant traits with moisture, maintaining DCCA Axis 2 (grazing) at a constant moderate value = 1. **B**. Variation of all plant traits with grazing, maintaining DCCA Axis 1 (moisture) at a constant moderate value = 2. Plots were drawn from the regression models (see Table 2), for weighted and simple averages and 95% confidence intervals are indicated with thinner lines. Values were plotted in their original scale by an exponential transformation for all cases except SLA which was not transformed. **C**. Differences between weighted and simple averages for all traits in the bidimensional space defined by both axes (W = weighted average, S = simple average).

sites. In other situations simple and weighted averages did not differ (Fig. 2 c).

Leaf toughness decreased with moisture, both considering the weighted and the simple average (Fig. 2a). The response to grazing varied according to which average was considered. Weighted average responded negatively, indicating that dominants had tougher leaves in light or ungrazed sites than in heavily grazed sites, while simple averages responded positively (Fig. 2b). The comparison between curves indicates that with low moisture and no/light grazing, the weighted average was significantly higher than the simple average, evidence that dominants were among the toughest species present in the community. As grazing and/or moisture increased, differences were progressively smaller until they became non-significant. Finally, at wet sites with heavy grazing, the differences were inverted, and simple averages became greater than weighted averages, indicating that dominants were among the softest species present in the community (Fig. 2c).

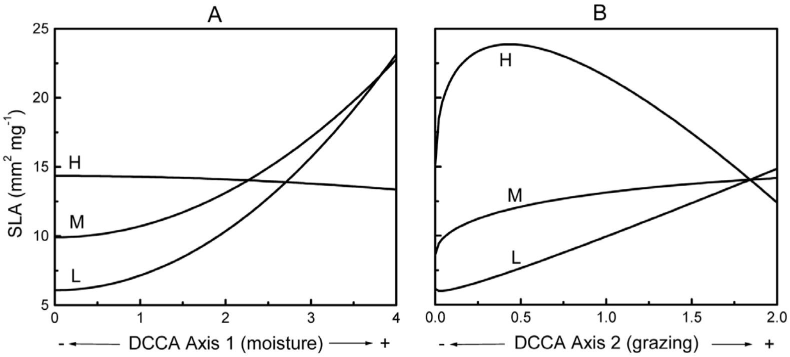

Fig. 3. **A**. Variation of SLA weighted average under different grazing pressures in function of moisture. H = heavy grazing, M = moderate grazing, L = light grazing. **B**. Variation of SLA weighted average under different moisture situations in function of grazing. H = high moisture, M = moderate moisture, L = low moisture. Curves were plotted from full models shown in Table 2, fixing grazing (score along DCCA Axis 2) and moisture (score along DCCA Axis 1), for A and B respectively, as constant maximum, medium and minimum values.

SLA showed interactions between both gradients in the case of weighted averages. At sites with moderate grazing, the weighted SLA average increased with moisture (Figs. 2a and 3a). This pattern was even more accentuated in the case of lightly grazed or ungrazed sites (Fig. 3a). However, as grazing increased from moderate to heavy, the responses of SLA weighted average to moisture became weaker, until at the heavily grazed sites the weighted average hardly varied with moisture (Fig. 3a). Grazing produced a positive response of SLA weighted average at mesic and xeric sites, and the response was stronger as xericity increase (Figs. 2b and 3b). At wet sites the relationship between grazing and SLA weighted average changed to unimodal, with a maximum at relatively light grazing (Fig. 3b). Simple averages responded positively to moisture, indicating that wet sites have a higher proportion of species with high SLA than xeric sites (Fig. 2a). At mesic/xeric sites with low to moderate grazing, and in extremely wet and grazed sites, weighted averages were greater than simple averages, indicating that dominants were among the species with the lowest values of SLA. At wet sites with moderate grazing, in contrast, SLA weighted average was greater than simple average. In all other situations, the averages did not differ (Fig. 2c).

Discussion

As predicted, we found that the responses of weighted averages were stronger than the responses of simple averages, and that the magnitude and sign of the differences between both were not consistent along the gradients. However, in contrast with our expectations, the trends of the responses were not always similar between averages. Similar trends appeared only in five out of ten possible cases (response of plant height, leaf area and leaf thickness to grazing and of leaf toughness and SLA to moisture). In three cases simple averages did not respond at all (plant height and leaf thickness to moisture and SLA to grazing), and in two cases we found qualitatively different response curves between the averages (leaf area and toughness in response to moisture and grazing respectively).

For traits most closely related with size (plant height, leaf area and leaf thickness), grazing represented a more consistent filter than moisture because it affected both averages in similar ways. For small species, the probability of occurrence (first-level filter), as well as the probability of attaining high abundance (first + second level) was higher under heavy than under light grazing, while the opposite happened with large species. Moisture, in turn, represented a less consistent filter for plant size, because it affected in different ways according to the particular trait and the level considered. For example, the stature and leaf thickness of a species did not affect its probability of occurrence at any condition of moisture, but affected its probability of becoming dominant. In the case of leaf area, increasing moisture filtered out species with small leaves, increasing the proportion of species with large leaves at the wet end of the gradient. However, species with the largest leaves become dominant at the centre of the gradient and not at the wettest end. The strong and consistent response of plant size to grazing is not surprising, since small size is traditionally associated with grazing resistance (Coughenour 1985; Milchunas et al. 1988) and is a widely reported characteristic of grazing increasers, both in studies at the community or at the species level (Dyksterhuis 1949; Noy-Meir et al. 1989; Díaz et al. 1992, 1994, 2001, 2007; Osem et al. 2004; Cingolani et al. 2005a, b; del Pozo et al. 2006). The less consistent response of plant size to moisture is more difficult to interpret because, in general, plant size increases with higher water availability (Fonseca et al. 2000; Ackerly et al. 2002; Osem et al. 2004). It is possible that trade-offs with other traits, together with the complexity of the moisture gradient which involves some stress at both extremes, are responsible of these patterns.

For traits most closely associated with the resource acquisition strategy (SLA and leaf toughness, Díaz et al. 2004) moisture represented a more consistent filter than grazing. Both the probability of occurrence and the probability of being dominant increased with increasing moisture for acquisitive plants (high SLA and soft leaves) and decreased for conservative plants. In contrast, grazing represented a less consistent filter. Although it is clear that grazing produced a replacement of conservative dominants by more acquisitive dominants in most situations, this replacement was not accompanied by an increase in the proportion of acquisitive species. Moreover, in the case of leaf toughness we found the opposite pattern (i.e. an increase in the proportion of species with tough leaves). The increase of acquisitive plants with moisture is as expected according to other studies at different scales and organization levels (Díaz et al. 1999, 2004; Fonseca et al. 2000; Wright et al. 2001; Ackerly et al. 2002; Grime 2006). The less consistent response to grazing could be related to the different plant strategies. While some plants resist grazing through tolerance, other plants resists through different mechanisms of avoidance (Rosenthal & Kotanen 1994). Both strategies are associated in general to a small size, but they are opposite in their resource acquisition attributes. While the tolerant strategy requires acquisitive tissues to sustain regrowth, the avoidant strategy needs conservative tissues to prevent plant consumption (Díaz et al. 2001; Cingolani et al. 2005a). In our case there is probably a mixture of strategies to cope with grazing among non-dominant species.

The main mechanisms involved in the filtering processes are physiological constraints and biotic interactions (Keddy 1992; Cornwell et al. 2006). Both mechanisms can probably operate at both levels, because a restrictive environment can completely exclude a species with unfitted traits or only prevent it attaining high abundance. Similarly, competition can produce exclusion or, alternatively, maintain less competitive species in low abundance. However, the way in which both mechanisms are related with the different traits is likely to have important consequences on which species (according to their trait values) are completely filtered out of a given environment and which ones are able to persist but not to dominate. This would determine how simple and weighted averages respond, producing convergent (qualitatively similar) or divergent (qualitatively different) curves. More research is required to determine whether divergent curves are frequent or not in nature, and experimental studies are needed to analyse the role of physiological constraints and biotic interactions in the filtering process, in relation to different traits.

The steeper slopes for weighted than for simple averages, associated with large differences in the magnitudes between both averages for some environmental conditions, suggest that the second-level filter (which determines the probability of becoming dominant) is much stronger than the first (which determines the probability of presence). This confirms the idea that, at least at relatively local scales such as that of the present and other studies (e.g. Ackerly et al. 2002), the trait values and combinations that a species needs to be dominant are more restricted than those necessary to be present in a community. This is in line with other studies showing a high variability in trait values within a community (Leishman & Murray 2001; Gurvich et al. 2003). The different curves obtained for simple and weighted averages imply that the sign and/or magnitude of differences between them vary at different sectors of the gradients. The larger is the absolute difference between curves, the stronger is the second-level filter in relation to the first at that particular combination of environmental conditions. For most traits, we found that the characteristics of species favoured by the second-level filtering can be contrasting and environment dependent. For example, at the most xeric and least grazed sites, weighted averages were much greater than simple averages for plant height and leaf toughness, meaning that, independently of how species were sorted at the first level, at the second level dominance was favoured for the tallest and toughest species able to be present in the community. At heavily grazed and moist situations, the shortest and softest species able to be present in the community were those with the highest capacity to become dominant.

Our results, showing different response curves for the two averages, suggest that caution is in order when making conclusions about the influence of environmental constraints on the assemblage of communities based on species traits. For example, Shipley et al. (2006) developed a procedure to predict species assemblages which combine random processes with environmental constraints. Following this procedure, the relative abundance of all species in a community was predicted on the basis of their trait values and environmental constraints, including zero (absence) only as a category of abundance. Predictions were very accurate on a quantitative basis, but were not accurate enough to differentiate absence from low abundance, as judged by the plots (see Fig. 2 in Shipley et al. 2006). This confirms our idea that the same principles are not always applicable in the understanding and prediction of the assemblage mechanisms at both levels. In another recent work, Cornwell et al. (2006) proposed a framework to measure the strength of habitat filtering. Their approach was based on the estimation of the multidimensional volume (convex hull volume) of trait values at different environmental situations. This procedure is valid because it considers the whole range of variation of plant traits on a multidimensional basis, and not only the average values of each trait independently, as we have done. However, the convex hull volume methodology is valid only in detecting the environmental constraints on plant attributes at the first level, because it is based on presence-absence data. The present challenge would be to better understand the ecological mechanisms involved in the filtering at both levels and find methodological alternatives to detect constraints and predict species assemblages recognizing both level filters as two different, but closely linked, processes.

Acknowledgements We thank I. Noy-Meir, P.A. Tecco, S. Münzbergova and two anonymous reviewers for critical reading of, and helpful suggestions on, an early version of this manuscript, and to the authorities of Quebrada del Condorito National Park for permissions. The research was supported by Agencia Córdoba Ciencia S. E., CONICET, FONCyT, Inter-American Institute for Global Change Research (CRN 2015; NSF Grant GEO-0452325), and the University of Córdoba.

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Received 23 October 2006;
Accepted 22 March 2007:
Co-ordinating Editor: M. Pärtel.