Disentangling plant trait responses to livestock grazing from spatio-temporal variation: the partial RLQ approach

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Abstract

Questions: Which plant traits consistently respond to grazing in different years and across habitat-related environmental heterogeneity? Does the proposed partial RLQ approach allow partitioning of grazing-related environmental parameters from other environmental and temporal variations?

Location: Semi-arid savannas of central Namibia.

Methods: We recorded nine quantitative and 12 categorical traits from 87 plant species along grazing gradients in semi-arid Namibian rangelands. We sampled from gradients in different habitat settings in 2 yr with differing total rainfall amounts. We first examined trait–environment relations with RLQ analysis. To remove confounding effects of temporal and habitat-related environmental variation on trait performance, we introduced a novel partial RLQ analysis approach. Furthermore, we used the fourth-corner statistic to quantify and test relations between traits, environmental factors and RLQ axes.

Results: Habitats and years had strong influences on trait patterns. After removing environmental variation caused by habitats and years, grazing became the most influential factor on trait responses. Traits negatively correlated with increasing grazing pressure were common to perennial grasses, such as long and entire leaves, anemochorous dispersal and rhizomatous growth. Positively correlated traits were those common to herbaceous, annual plants with a prostrate–creeping habit, compound leaves, high specific leaf area (SLA) and exo- or endozoochorous dispersal. Some previously acknowledged grazing response traits, like growth form and plant height, were strongly influenced by variations in habitats and years and showed no significant correlation with grazing pressure.

Conclusion: We emphasize that some traits that respond to grazing may also vary under different habitat conditions and among years, especially in highly variable environments like semi-arid savannas. When analysing trait–environment relations we recommend using approaches that partition environmental variation, particularly when applying broad sampling schemes at larger geographical scales.

Introduction

Exploring the relationship between environment and species traits facilitates general statements about the response of organisms to environmental constraints, beyond statements based solely on taxonomy. Such an understanding of an organism response to environment is necessary to generate predictive models of ecological community response to environmental changes (Keddy 1992). In many ecosystems, one important ecological driver causing environmental change is grazing by domestic and wild ungulates (Wardle & Bardgett 2004). With the aim of generalizing vegetation responses to grazing, trait-based approaches have been applied by a number of researchers (e.g. Landsberg et al. 1999; McIntyre & Lavorel 2001; Cingolani et al. 2007). Grazing response traits reflect

adaptations to various grazing regimes and thus could represent the key responses of vegetation at various scales from ecosystems to landscapes, biomes and continents (Lavorel et al. 2007). Increasing evidence suggests that at all scales and in any part of the world, single traits or a set of co-occurring traits can serve as indicators for changes in vegetation due to livestock grazing (Diaz et al. 2007).

In order to study grazing-induced changes in plant species composition, vegetation structure, diversity patterns or soil parameters the piosphere approach has been frequently applied in studies in many semi-arid regions around the world (Perkins & Thomas 1993; Landsberg et al. 2003; Todd 2006; Sasaki et al. 2008). Piospheres are zones of animal impact around artificially created livestock watering points (Lange 1969). They represent natural experiments comprising a gradual decrease in livestock impact with increasing distance from the water source (Andrew 1988). Hence, the piosphere approach implies sampling of vegetation or soil parameters along continuous grazing gradients. However, most studies of piospheres have focused on species responses, whereas few trait-based studies have been conducted, often restricted to a few, very general traits, such as growth forms and life cycle (see Skarpe 2000; Todd 2006; Sasaki et al. 2008).

One key issue of trait-based approaches has been methods of selecting traits and testing their relevance in relation to grazing response. Growth forms, for example, correspond to *a priori* (deductively) selected functional groups representing a combination of several subordinate traits or attributes (height, longevity, architecture, rooting depth, etc.). With regard to trait responses along grazing gradients, one could expect a more gradual change in single attributes, which probably remains obscured if only considering shifts in growth form. Further, deductive sampling of only a few traits relying on previous findings of trait responses studied elsewhere often neglects the specific environmental settings and the evolutionary history of the study region. Hence, the selection of a larger set of traits, i. e. a more inductive trait sampling strategy (*sensu* Gitay & Noble 1997), would help to reduce subjectivity, test the relevance of a broader trait spectrum and also consider unknown or unexpected environmental effects.

The sampling of grazing gradients at a regional scale often means dealing with environmental complexity, i.e. changes related to different landscapes, habitats and soils. If studying functional responses to grazing with the aim of achieving consistent results on a regional level, various environmental filters affecting trait assembly have to be taken into account. In order to classify the proportional effects of these filters on the occurrence of different traits or groups of traits, an adequate methodology to analyse trait–environment relationships is required. The difficulty in finding a direct means of relating trait variations in spe-

cies, species composition and environmental parameters has been described as the 'fourth-corner problem' (Legendre et al. 1997). Some suggestions to solve this problem have been made (Pillar 1999; Nygaard & Ejrnaes 2004). However, recently, two methodological approaches have been increasingly used (e.g. Aubin et al. 2009; Lacourse 2009; Römermann et al. 2009; Pakeman & Marriott 2010): RLQ – a three table ordination developed by Dolédec et al. (1996), and the fourth-corner analysis (Legendre et al. 1997) – a method to measure and test the direct correlation between a single trait and a single environmental variable. The latter method was extended by Dray & Legendre (2008) to deal with species abundances instead of mere presence–absence data. RLQ analysis and the fourth-corner statistic represent straightforward methods for exploring trait–environment relationships, and complement each other in terms of result interpretation (ordination and testing procedures). However, these methods still do not allow for controlling the effects of different environmental filters at various scales.

In the present study, we investigated the influence of livestock grazing on the distribution of plant traits in a semi-arid African savanna ecosystem. We sampled a large set of plant traits along piosphere transects in Namibian rangelands at a regional scale and analysed their grazing responses using RLQ analysis and the fourth-corner statistic. As recommended by Andrew (1988), we studied a range of piospheres with different stocking densities; moreover, sampled piospheres were also located in different habitats. The habitats mainly differed in soil conditions, corresponding to rangeland classification schemes used by the local farmers. Furthermore, our sampling was carried out in 2 yr that differed significantly in total rainfall amount, leading to differences in plant occurrences and biomass production. Differences in habitats and available moisture (rainfall) would presumably mask the grazing effect on trait patterning and lead to misinterpretations of RLQ and fourth-corner analysis outputs. Until now, such sources of variation have rarely been taken into account in analyses of trait–environment relationships. Rather, they have been excluded from sampling in order to avoid confounding effects, which is neither always intended nor feasible when recording ecological data sets at larger spatial scales and over a longer time periods. Here, we propose the use of partial RLQ – a new approach that partitions environmental heterogeneity in RLQ analysis. With this approach, we aimed to disentangle trait responses to grazing by separating explanatory variables related to habitat differences and different sampling years from other variables representing processes related to livestock activities. We therefore introduced a factor to stratify our samples according to habitats and years. Using this factor as covariable in the partial RLQ analysis, our main questions were:

(1) whether the newly proposed partial approach allows the partitioning of grazing-related environmental parameters from other environmental and temporal variations; and (2) which plant traits correlate with variables related to grazing pressure, representing a consistent grazing response across varying habitats and the two sampling years.

Methods

Study area

Our study area comprises ten farms in central Namibia, southern Africa (Fig. 1) near the town of Rehoboth (23.3° S, 17.1°E). It is located in the Namibian Central Highland foothills (ca. 1400 m a.s.l.) with a relatively flat topography and scattered mountainous terrain. The climate is semi-arid, with an average annual rainfall ranging from 200 to 300 mm, typically occurring during the summer

months of Dec to Mar. The rainfall is highly variable spatially and temporally, with a coefficient of variation of up to 40% (Mendelsohn et al. 2002). The average daily temperatures range from 17 °C in the winter months to 25 °C in summer. Soils vary from sandy to loamy. Dominant soil types are deep arenosols, shallow leptosols, calcisols and regosols. The study sites belong to the Nama-Karoo biome of southern Africa (Rutherford & Westfall 1994). The area was classified by Giess (1971) as a transition zone between different types of savanna: the Namibian Highland savanna in the north, the mixed tree and shrub savanna in the east and the dwarf shrub savanna in the south. The vegetation can be described as open shrub or dwarf shrub savanna with scattered trees, the latter occurring mainly along seasonal watercourses. As a part of the Nama-Karoo, the study area has a long history of grazing by large mammalian herbivores (Owen-Smith & Danckwerts 1997). Nowadays, livestock farming on privately owned farms

Fig. 1. Map of the study area in central Namibia (grey rectangle in the insert, top right). Stratification of the watering points and surrounding piospheres according to the habitat-year factor (for explanations see text): calcareous = TSW1, TSK1; stone = DAW2, KAW2, MAW3; sand 2007 = NAW1 & 2, DUW1, MAW1 & 2, KWW2; sand 2008 = TJW1, TSW2, KOW2.

with cattle, sheep and goats and game farming of antelopes are the dominant types of land use. Farm size is mostly small (<3000 ha) when compared to the average size of private Namibian farms (Lang 2005). Since farming is often the most important source of income, land degradation due to overstocking is a widespread problem in this low-carrying capacity, semi-arid rangeland, especially on smaller farms.

Piosphere selection

Field sampling was conducted during the rainy seasons in 2007 and 2008 on ten farms, ranging from 2500 to 12 000 ha in size. On these farms, a total of 14 grazing gradients, i.e. piospheres, each situated in a fenced paddock, were sampled (Fig. 1). The paddocks, each with a permanent watering point, were 200 to 600 ha and had been constantly grazed (at least 1 mo per year) during the last 5 yr. The grazing season, however, differed between the chosen paddocks according to farm management and available grazing resources. Paddocks comprising steep slopes or major changes in landscape were avoided. In all sampled piospheres, the watering point was the only source of open water, with the exception of small drainages, which are water-bearing for only a short time during periods of heavy rain. The selection of piospheres followed the criteria used by local farmers to classify habitat types corresponding to different soil conditions, known locally as 'veld' types. Our selection aimed to represent the main habitat types in the area (Table 1). Some habitats are more frequent than others, which led to unequal numbers of piospheres per habitat in our overall sample. The habitat 'sand' was sampled in 2 yr that differed considerably in the amount of rainfall, having a major impact on biomass production and the occurrence of annual plants. We therefore decided to include a temporal factor in the stratification of our samples and split the samples accordingly. Thus, we created a categorical covariable named 'habitat–year factor' specifying for each sample the corresponding habitat and the sampling year (Table 1). This factor was used in the statistical analysis as a covariable in order to control for the effects of spatio-temporal variability on the trait–environment relationship.

Field methods and data preparation

Each piosphere around a watering point was concentrically divided into six zones (0–20 m, 20–80 m, 80–200 m, 200–400 m, 400–800 m, 800–1500 m). The limits of these zones were defined according to previous inspections of several piospheres in the study area. We assumed a more or less homogenous distribution of grazing pressure in each of the zones. The sampling only concerned the grazing gradient around the watering point, i.e. a maximum of 1500-m long, while the sampled paddocks often covered considerably greater areas of several hundred hectares. Except for the first zone (0–20 m), in all other zones five 10 m × 10 m plots were randomly placed and sampled. Due to space constraints, only one to three of such 10-m² plots could be placed in the first zone. On these plots ($n = 378$), vascular plant species composition (245 species) and percentage cover were recorded, resulting in a species-by-sample matrix. Cover values of the plant species were log-transformed.

For dominant and most abundant species (cover >0.1% and frequency within all samples >5%, if frequency <5% then maximum cover ≥3%), plant functional traits were recorded (Table 2). Cover values for those species included in the trait sampling summed up on each plot to more than 80% of the total vegetation cover. Traits sampled are primarily those that have been described as important in terms of disturbance/grazing response (Weiher et al. 1999; Diaz et al. 2007). However, many of the selected traits are also linked to the competitive ability of plants, or vary along axes of resource availability (Cornelissen et al. 2003). Plant traits were recorded once from one population in the study area. We measured traits from ten average-sized adult plant individuals per species growing with good vigour at the peak of the growing season or towards its end. Trait variability among the different populations of the study area was assumed to be minimal. Thus, the mean values of quantitative traits taken from the ten individuals of a species are regarded as representative for the species in the overall sample. Measurements of leaf traits (see Table 2) included the leaf blade and petiole. The species-by-trait matrix included 87 plant species, nine quantitative traits and 12 categorical traits (App. S1). Classes within categorical traits summed to 45 trait attributes (Table 2).

Table 1. Stratification of the samples according to the habitat-year factor, number of sampled piospheres and plots (in brackets) per habitat and year, with a short characterization of the habitats.

Habitat name (Habitat-year factor)	Description of soils	Sampling year	Rainfall	Number of piospheres (number of plots)
Calcareous	Shallow soils with calcretes	2008	High	2 (55)
Stone	Shallow stony soils, leptosols	2008	High	3 (80)
Sand07	Deep sandy soils	2007	Low	6 (162)
Sand08	Deep sandy soils	2008	High	3 (81)

Table 2. Plant functional traits used in the **Q**-table: abbreviations, attributes of categorical traits and units for quantitative traits. Quantitative traits are marked with (quant).

Traits	Abbreviation	Trait attributes of categorical traits, units of quantitative traits
Whole plant traits		
Life cycle		Annual, weak perennial, perennial
Growth form		Tree, shrub, dwarf shrub, grass/sedge, woody forb, herbaceous forb
Habit (including aspects of shoot architecture)		Upright, compact, cespitose (graminoids only), rhizomatous (graminoids only), prostrate, prostrate/creeping, rosette
Height (quant)		Plant maximum height (cm)
Above cover density (quant)	ACD	Percentage cover of the plant canopy above a vertically projected contour of the plant
Stem–Leaf Ratio		Leafy, moderately leafy, not leafy
Spinescence		None, sparse, intermediate, dense
Spine length (quant)		Spine length (mm)
Hairiness		None, sparse, intermediate, dense
Waxes		Yes, no
Leaf traits		
Leaf blade fragmentation		Entire, compound
Leaf consistency		Soft mesomorphic, hard mesomorphic, scleromorphic, leathery, sub-succulent
Ratio leaf length/width (quant)	Leaf ratio	Leaf length (mm) divided by leaf width (mm)
Leaf height (quant)		Leaf height (thickness) (mm)
Leaf area (quant)		Leaf area (mm²)
Specific leaf area (quant)	SLA	Specific leaf area (mm²·mg^{-1}), i.e. leaf area divided by dry weight of the leaf
Regenerative traits		
Flower position		Exposed, not exposed
Diaspore length (quant)		Length of diaspore (mm)
Seed length (quant)		Length of seed (mm)
Dispersal		Autochorous, anemochorous, endozoochorous, exozoochorous
Clonality		None, above-ground clonality, below-ground clonality

The quantitative parameters listed in Table 3 served as environmental variables. Some of these variables showed greater variation within sites while others differed more between sites.

Soil depth was an average of four measurements per plot using a metal bar and a hammer. The other soil parameters were measured in a mixed soil sample consisting of five subsamples taken from the topsoil layer (10 cm) on each plot. The skeleton content of each mixed soil sample was removed using a 2-mm sieve, and weighed. The pH was determined in a suspension of 10 g dry soil with 25 ml 0.01 M CaCl₃ solution using a pH electrode. Electrical conductivity was measured with a conductivity sensor, in a suspension of soil and distilled water at a ratio 1:2.5. All other soil chemical parameters were measured by ion-exchange chromatography from a 1 g subsample that was sieved to 1 mm.

We used distance from watering point as a proxy for grazing pressure, which has been proved useful in many studies (e.g. Landsberg et al. 2003; Todd 2006; Sasaki et al. 2008). Additionally, we defined the parameter grazing intensity (*GrazInt*, equation 1).

$$GrazInt = (SR \times logDist \times PioProp)^{-1} \qquad (1)$$

This parameter was calculated using the average stocking rate of the last 5–7 yr in each paddock (*SR* in ha per livestock unit per year), distance from the watering point (*logDist*, natural logarithm of distance in m) and the proportion of a full circle with a radius of 1500 m around each watering point (*PioProp*) that is accessible to livestock. By using the parameter grazing intensity, we aimed to include additional information besides the distance from the watering point that influence the grazing pressure at any given point. Grazing intensity was thus a parameter showing variations also between differently managed farms (different stocking rates). Furthermore, different spatial layouts of paddocks (e.g. watering points in the centre of a paddock vs watering points at a sharp angle of a paddock) and physical barriers (e.g. small rock outcrops) that would influence the distribution of livestock grazing pressure (cf. Pringle & Landsberg 2004) are taken into account.

Data analysis

The data were analysed by means of RLQ analysis (Dolédec et al. (1996). RLQ analysis relates a matrix of environmental variables by samples (**R**-table) to a species-by-traits matrix (**Q**-table) using a species-abundance, or in our case a species-cover-by-samples matrix (**L**-table) as a link. As an extension of co-inertia analysis, RLQ is less sensitive to the number of input variables compared to other

Table 3. Environmental variables used in the **R**-table: categories, abbreviations, descriptions and units.

Abbreviation	Environmental variable
Grazing parameters	
logDist	logarithm of distance from watering point (m)
GrazInt	Grazing intensity (for method of calculation see text)
Soil chemical parameters	
pH	pH value (measured in $CaCO_3$)
Conductivity	Conductivity ($\mu s \cdot cm^{-1}$)
Cl	Chloride (ppm)
NO_2	Nitrite (ppm)
NO_3	Nitrate (ppm)
PO_4	Phosphate (ppm)
SO_4	Sulphate (ppm)
Na	Sodium (ppm)
NH_4	Ammonium (ppm)
K	Potassium (ppm)
Mg	Magnesium (ppm)
Ca	Calcium (ppm)
Soil physical parameters	
Skeleton	Skeleton fraction of the soil (%), i.e. particles >0.2 cm
Soil depth	Soil depth (cm)
Soil surface parameters	
Fine	Cover of fine material <0.2 cm (%)
Gravel	Cover of gravel 0.2–2.0 cm (%)
Stones	Cover of stones >2 cm (%)
Blocks	Blocks >60 cm (%)
Wood	Cover of dead wood (%)
Litter	Cover of litter (%)
Dung	Cover of dung (%)
Biocrust	Cover of biological soil crust (%)
Topographical parameters	
Inclination	Inclination (%)

ordination methods (see Dolédec & Chessel 1994; Dray et al. 2003).

Prior to RLQ analysis, all tables were subjected to separate ordinations. Correspondence analysis (CA) was computed on the species-by-sample matrix (**L**-table). The matrix of environmental variables by samples (**R**-table) was analysed with a standardized principal components analysis (PCA). For the species-by traits matrix (**Q**-table), a Hill and Smith ordination (Hill & Smith 1976) was performed for mixed quantitative and categorical variables. Sample scores from the CA of the **L**-table were used as row weights in the PCA of the **R**-table, and species scores from the CA of the **L**-table were used as row weights in the ordination of the **Q**-table. RLQ analysis is an extension of co-inertia analysis, which simultaneously takes into account the information contained in the tables **R**, **L** and **Q** (Dray et al. 2003). In the RLQ analysis, the **L**-table represents the magnitude of the relationship between environmental variables and species traits, i.e. the method seeks a linear combination of traits (species score) and a linear combination of environmental variables (sample score) that maximize the covariance measured through the **L**-table.

After performing a regular RLQ (referred to as 'basic RLQ'), we carried out a partial analysis (referred to as 'partial RLQ') to control for the effect of the habitat-year covariable. If we assume that covariables appear as columns in a table **W** with the sites as rows, partial RLQ is performed in two steps: (1) compute two multivariate regressions using **W** as an explanatory table and **R** and **L** as response tables; the residuals of these models are shown in tables R_r and L_r, respectively; (2) compute a slightly modified RLQ analysis using the original table **Q** and the tables R_r and L_r instead of **R** and **L**. In this new analysis, the variation in **R** and **L** that is linked to **W** has been removed. The input variables, i.e. species, traits and environmental variables of the basic and the partial RLQ, were exactly the same. However, by using the habitat-year factor in the partial RLQ we aimed to remove the variation that is linked to this factor within all variables, i.e. differences in main habitat types and different sampling years. This corresponds to a particular case of the partial RLQ, where the covariable (habitat-year) represents a partition into groups (within-analysis, Dolédec & Chessel 1987). This analysis (function *wca.rlq*) is implemented in the ade4 package (Dray & Dufour 2007). Comparing the contribution to total inertia of each environmental variable in the basic and the partial RLQ reveals the most important environmental gradients in each analysis. Further, the contribution to total inertia can also be used as a measure of relevance of traits when comparing the results of the basic and the partial RLQ.

To quantify the relationship of environmental variables with the axes of the partial RLQ, we used the fourth-corner statistic (Dray & Legendre 2008). Environmental variables contained in table R_r (i.e. controlled for the habitat-year covariable) were tested against the species scores of the partial RLQ axes, which can be regarded as synoptic vectors representing linear combinations of the traits. Obtained correlations thus measure the link between each environmental variable and trait variation across the habitat-year factor. The significance of correlations was tested with 999 permutations using two different permutation models (see Dray & Legendre 2008 for details). Whether species assemblages are dependent on environmental characteristics of the locations where they are actually found (permutation of the site vectors in the **L**-table, model 2 in Legendre et al. 1997) was tested in the first model. In the second model, the permutation procedure tested whether the distribution of species depends on the traits these species possess (permutation of the species vectors of the **L**-table, model 4 in Legendre et al. 1997). As proposed by Dray & Legendre (2008), the two models were combined in order to attain the correct level of Type I error. Here, we considered a trait to be significantly correlated if both *P*-values associated to models 2 and 4 were lower than $\alpha = 0.05$.

In the same way, the relationship between traits and environmental gradients corresponding to the partial RLQ axes was tested. In this case, we used the site scores of the partial RLQ axes as synoptic environmental vectors representing linear combinations of environmental variables, controlled for the habitat-year factor. Again, the significance of correlations between traits and partial RLQ axes was tested with 999 permutations using model 2 and model 4 described in Legendre et al. (1997), which were then combined. The *P*-value of the combined approach was again compared at $\alpha = 0.05$.

We were mostly interested in the correlations of environmental variables and traits with the partial RLQ axes representing vectors controlled for the habitat-year effect. However, to facilitate a better comparison between basic and partial RLQ we also calculated fourth-corner correlations for the original tables **R** and **Q** with the first two axes of the basic RLQ using the same testing procedure as used for the partial RLQ. All data were analysed using the ade4 library (Dray & Dufour 2007) in the open source R environment version 2.8.0 (R Development Core Team 2008, R Foundation for Statistical Computing, Vienna, Austria).

Results

Basic RLQ vs partial RLQ

The percentage of total co-inertia (i.e. link between the traits and environmental variables) explained by the first two axes of the basic RLQ was 76%, and 86% for the partial RLQ (Table 4). The first axis of the basic RLQ explained 46%, whereas the percentage of co-inertia explained by the first partial RLQ axis was much higher (72%). This indicated the relevance of a more pronounced environmental gradient along the first axis of the partial RLQ when compared to the basic RLQ. In the ordination diagram of the basic RLQ (large plot in Fig. 2) there is a noticeable grouping of samples. Especially the sampling year had an enormous influence on the ordination, since most of the samples of 'sand 2007' clustered in the left half of the ordination diagram of the basic RLQ, and all samples of 'sand 2008' in the right half. This pattern changes in the partial RLQ (small plot in Fig. 2), where clusters of samples are broken up and no grouping of samples according to the habitat-year factor could be found.

Environmental variables

In terms of contributions to total inertia, cover of litter was the most important environmental variable in the basic RLQ, and it was the variable showing the highest correlation with the first basic RLQ axis (Table 5). However, this variable was shown to be nearly irrelevant in the partial RLQ. Cover of litter is related to annual biomass production and as such is subject to strong inter-annual fluctuations. Similarly, soil depth, content of soil skeleton material and cover of gravel were important in the basic RLQ, but were of reduced importance in the partial RLQ. These variables mainly represent characteristics of different habitats. Conversely, the variables distance from watering point, dung cover, conductivity, grazing intensity and pH almost doubled in importance in the partial RLQ when compared to the basic RLQ (Table 5). The variables that gained importance in the partial RLQ may be most related to livestock activities such as grazing, urination and defecation.
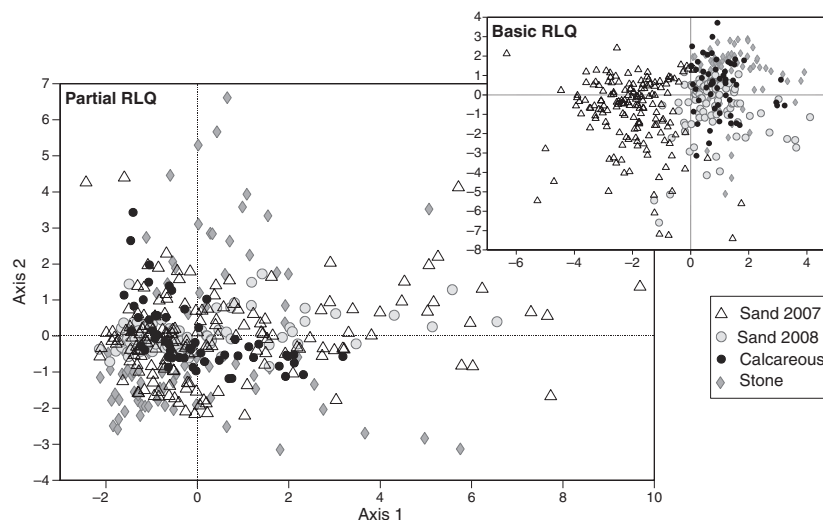
Fig. 2. Sample scores (378 vegetation samples) of the first two axes of the partial RLQ (large plot) and the basic RLQ (small plot, top right). The samples are marked after the habitat-year stratification. For eigenvalues of the basic and the partial RLQ, see Table 4.

Table 4. Eigenvalues, percentage and cumulative percentage of variance (cum.%) explained by the first five axes of the basic RLQ (sum of eigenvalues: 4.325) and the partial RLQ (sum of eigenvalues: 1.795).

Axis	Basic RLQ			Partial RLQ		
	Eigenvalue	%	Cum.%	Eigenvalue	%	Cum.%
1	1.886	43.6	43.61	1.293	72.0	72.00
2	1.418	32.8	76.39	0.257	14.3	86.31
3	0.541	12.5	88.89	0.087	4.8	91.15
4	0.227	5.3	94.15	0.046	2.6	93.70
5	0.111	2.6	96.72	0.028	1.5	95.24

In the fourth-corner statistic, correlations between environmental variables and RLQ axes were not very high (Table 5). However, we attached particular importance to the significance of correlations since our testing procedure was very conservative (Dray & Legendre 2008 proposed comparing the P-value of the combined approach to the square root of 0.05, whereas we used $\alpha = 0.05$ instead). The first basic RLQ axis was significantly correlated with cover of litter and gravel and several soil nutrients (especially PO_4, K and NH_4). The second axis showed significant correlations to grazing-related variables like distance from watering point, dung cover and grazing intensity, but also soil depth, SO_4 and cover of fine material were significantly correlated (Table 5).

In the first partial RLQ axis, distance from watering point (negatively correlated), dung cover, conductivity, grazing intensity and pH (positively correlated) showed the highest significant correlations (Table 5). Hence, the

Table 5. Percentage contribution to total inertia of the basic and the partial RLQ (each column sums up to 100%) and Pearson correlations (r) of environmental variables with axes 1 and 2 of the basic and partial RLQ according to the fourth-corner statistic (combination of models 2 and 4, after Dray & Legendre 2008).

Environmental Variable	Contribution to total inertia [%]		Correlation r with basic RLQ axes		Correlation r with partial RLQ axes	
	Basic RLQ	Partial RLQ	Axis 1	Axis 2	Axis 1	Axis 2
Grazing parameters						
logDist	11.94	27.44	−0.097	0.323***	**−0.338*****	0.063
Grazint	4.17	8.47	0.009	−0.161**	**0.148****	**0.106***
Soil chemical parameters						
Conductivity	3.31	10.3	−0.027	−0.138*	**0.212*****	−0.005
pH	4.73	7.79	−0.001	−0.027	**0.213****	0.099
SO_4	1.84	3.03	0.033	−0.129***	**0.108*****	−0.035
NO_3	2.63	2.91	−0.118***	−0.095**	**0.102*****	0.011
NH_4	3.19	1.36	−0.16***	−0.05	**0.053***	0.034
PO_4	5.43	1.21	−0.217***	−0.054	**0.058***	−0.022
Ca	3.12	1.21	0.12	0.028	**0.052***	0.052
Cl	0.86	0.87	−0.069*	−0.045*	0.04	−0.036
Na	1.56	0.5	0.113***	−0.024	0.019	0.006
K	3.44	0.49	0.174***	−0.032	0.029	−0.002
Mg	2.28	0.48	0.141***	−0.004	0.005	−0.017
NO_2	0.22	0.46	0.012	−0.008	−0.016	−0.013
Soil physical parameters						
Soil depth	7.07	2.09	0.14	−0.161*	0.004	**0.118****
Skeleton	4.61	1.54	0.149*	0.125*	**−0.069***	**0.114****
Soil surface parameters						
Dung	6.23	14.24	−0.014	−0.24***	**0.239*****	−0.058
Biocrust	2.86	3.23	−0.117***	0.077*	−0.05	**0.1****
Stones	3.53	2.98	0.024	0.118	−0.006	**0.141*****
Wood	2.33	2.17	−0.122***	0.029	−0.034	**0.075****
Fine	4.23	1.65	−0.108*	−0.15**	**0.115*****	−0.026
Gravel	5.71	0.99	0.198***	0	−0.014	**−0.06***
Litter	12.52	0.5	−0.346***	0.005	−0.014	0.015
Blocks	0.25	0.35	−0.009	0.036	−0.027	−0.009
Topographical parameters						
inclination	1.93	3.73	0.014	0.082*	−0.044	**0.159****

Significance codes: *$P < 0.05$; **$P < 0.01$; ***$P = 0.001$.
Variables significantly correlated with partial RLQ axes are shown in bold. Variables within categories are ordered according to their contribution to total inertia of the partial RLQ.

first axis of the partial RLQ represented a grazing gradient, with low grazing influence on the negative side and high grazing influence on the positive side of the axis. Other variables significantly correlated with the first axis, though less important in terms of contribution to total inertia, were SO_4, NO_3, cover of fine material, skeleton content, NH_4, Ca and PO_4.

Grazing intensity was significantly correlated with the second partial RLQ axis. Beside its importance in the first axis as a 'grazing parameter', grazing intensity also corresponds to differences between farms, since it comprises the spatial arrangement of the piospheres and management practices. Other variables significantly correlated with the second partial RLQ axis were inclination, cover of biological soil crusts, stones and wood, soil depth and skeleton content, representing either topographical or soil-related parameters, indicating differences between habitat types. In summary, the first basic RLQ axis mainly signified changes in variables related to habitats and years, and the second basic RLQ axis represented a mixed gradient of grazing parameters and other environmental variations. The first partial RLQ axis was identified as a 'grazing axis', while the second axis highlighted the differences between farms, including different habitats.

Quantitative and categorical traits

As shown in the previous section, grazing is particularly relevant in the partial RLQ. With regard to traits, we will therefore refer mainly to the results of the partial RLQ and the fourth-corner analysis with the partial RLQ axes (contributions of traits to total inertia and all fourth-corner correlations of traits with basic and partial RLQ axes are reported in Table 6).

Among the quantitative traits, ratio of leaf length to width (leaf ratio) showed a negative, and specific leaf area (SLA) a positive significant correlation with the first partial RLQ axis, while above-ground cover density (ACD) showed a positive and significant correlation with the second axis (Table 6). At the level of whole categorical traits, life cycle, leaf blade fragmentation, dispersal mode and clonality were significantly correlated with the first axis of the partial RLQ (Fig. 3). There was no significant correlation between whole categorical traits and the second axis of the partial RLQ. At the attribute level of the categorical traits, prostrate–creeping habit, compound leaf blade, herbaceous forb as growth form, annual life cycle, endo- and exozoochorous dispersal and the absence of clonality showed positive and significant correlations with the first axis of the partial RLQ (Table 6). Plants having below-ground clonality, perennial life cycle, anemochorous dispersal, rhizomatous habit, leafy stems and entire leaf blades were negatively correlated with the first partial RLQ axis. The

tree growth form was the only attribute of the categorical traits significantly correlated with the second axis of the partial RLQ (Table 6). With one exception (entire leaf blade), the quantitative traits and trait attributes that showed a significant correlation with one of the first two partial RLQ axes were also the most influential in terms of contribution to total inertia in the partial RLQ.

Discussion

Partitioning of environmental variation

Basic RLQ analysis revealed that trait variation in our sample was driven by grazing-related environmental variables as well as variables related to habitat, year and most probably management. Regarding the hierarchy of variables with respect to their allocation to basic RLQ axes, our results suggest that at the given spatial and temporal scale of sampling, environmental filtering of traits was foremost driven by variables related to temporal changes and habitats. Hence, the influence of grazing on trait distribution was masked by other environmental variations. With the help of the partial RLQ analysis we were able to remove confounding environmental variation and to uncover the grazing influence. The result was a 'grazing axis', i.e. the key environmental variables on the first partial RLQ axis were all related to livestock activities (Table 5).

Distance from watering point turned out to be the most important environmental variable in the partial RLQ. This parameter, or its inverse, has been used in many other studies as a direct proxy for grazing pressure (e.g. Perkins & Thomas 1993; Skarpe 2000; Todd 2006; Manthey & Peper 2010). Although distance from watering point had a strong influence on trait distribution in both analyses, the basic and the partial RLQ, it was subordinate in the basic RLQ and only dominated on the second axis (Table 5). This suggests cautious use of this parameter as a direct measure of grazing pressure, when other environmental variations may exert a greater influence on biotic response variables. In the absence of any analytical step filtering out confounding variables, samples from different locations should be treated independently (see Sasaki et al. 2008). Hence, in accordance with Pringle & Landsberg (2004), we conclude that it is a matter of spatial scale as to whether distance from water can be used as a simple surrogate for grazing pressure.

Closer to watering points, dung cover, electrical conductivity and soil pH all increased. These parameters were most influential on trait variability along the first axis of the partial RLQ in the opposite direction of distance from watering point. Dung accumulation is considered to be a good correlate of time spent by animals at a given locality (Andrew 1988). Higher pH and lower soil resistance values, i.e. the inverse of conductivity, in the vicinity of

Table 6. Percentage contribution to total inertia of the basic and the partial RLQ (each column sums up to 100%) and Pearson correlations (r) of quantitative traits/attributes with axes 1 and 2 of the basic and partial RLQ according to the fourth-corner statistics (combination of models 2 and 4, after Dray & Legendre 2008).
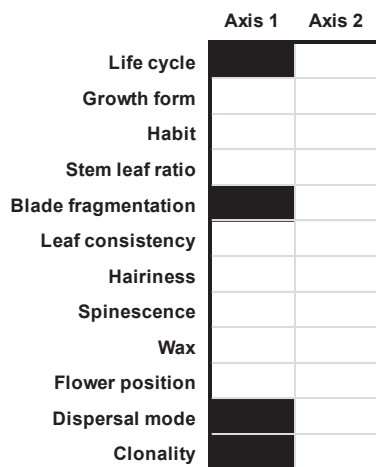
Traits/attributes		Contribution to total inertia [%]		Correlation r with basic RLQ axes		Correlation r with partial RLQ axes	
		Basic RLQ	Partial RLQ	Axis 1	Axis 2	Axis 1	Axis 2
Quantitative traits							
	Leaf ratio	2.8	6.75	0.049	0.196***	**−0.213*****	−0.011
	SLA	4.67	4.19	0.135	−0.183**	**0.159***	−0.058
	ACD	1.64	2.47	−0.042	0.084	−0.066	**0.123****
	Leaf height	1.33	2.62	−0.053	−0.121	0.117	0.065
	Height	3.24	1.54	−0.187**	0.017	−0.006	0.112
	Leaf area	1.08	1.06	−0.098	−0.05	0.046	0.051
	Diaspore length	2.86	0.75	−0.155*	−0.084	0.027	−0.005
	Seed length	1.77	0.5	−0.143	0.029	−0.032	0.027
	Spine length	2.24	0.32	−0.15*	−0.036	0.004	−0.036
Categorical traits							
Life cycle	Annual	7.03	4.21	0.313***	−0.196**	**0.185****	−0.086
	Perennial	3.49	3.96	−0.244**	0.255***	**−0.249*****	0.077
	Weak perennial	1.79	2.29	−0.072	−0.113	0.119	0.005
Growth form	Herbaceous forb	3.14	4.42	0.112	−0.2**	**0.18****	−0.035
	Tree	2.08	4.07	−0.075	−0.028	0.086	**0.169***
	Shrub	3.86	1.15	−0.214**	0.01	−0.059	−0.055
	Grass/sedge	1.41	1	0.169*	0.128*	−0.117	−0.033
	Dwarf shrub	2.28	0.98	0.007	0.098	−0.038	0.059
	Woody forb	2.3	0.94	−0.156*	−0.072	0.053	0.027
Habit	Prostrate–creeping	3.3	6.47	0.108	−0.188*	**0.21****	−0.049
	Rhizomatous	1.72	3.33	0.036	0.172***	**−0.157***	−0.026
	Compact	1.73	0.79	−0.09	0.026	0.007	0.061
	Upright	2.32	0.28	−0.184*	−0.048	0.009	0.026
	Prostrate	0.52	0.23	−0.062	−0.001	−0.027	0.004
	Cespitose	0.99	0.2	0.144	0.017	−0.016	−0.017
	Rosette	0.06	0.13	0.003	−0.009	0.006	0.017
Stem–leaf ratio	Leafy	1.51	2.49	0.096	0.155*	**−0.157***	0.079
	Moderately leafy	1.23	2.15	−0.074	−0.143*	0.142	−0.086
	Not leafy	0.69	0.74	−0.073	−0.039	0.048	0.024
Spinescence	Sparse	3.11	1.54	−0.16**	−0.125*	0.082	−0.013
	Strong	1.53	1.46	−0.122	−0.06	0.088	0.059
	None	0.81	0.48	0.202*	0.11	−0.116	−0.047
	Intermediate	0.55	0.24	−0.077	−0.018	0.012	−0.001
Hairiness	None	0.82	0.95	0.005	0.11	−0.076	−0.036
	Strong	2.49	0.87	0.122	−0.098	0.041	0.034
	Intermediate	1.49	0.66	0.118	0.012	0.058	0.032
	Sparse	1.89	0.18	−0.189*	−0.037	−0.014	−0.021

Table 6. *(Continued).*

Traits/attributes		Contribution to total inertia [%]		Correlation r with basic RLQ axes		Correlation r with partial RLQ axes	
		Basic RLQ	Partial RLQ	Axis 1	Axis 2	Axis 1	Axis 2
Wax	Yes	1.49	1.29	−0.084	−0.07	0.075	0
	No	0.09	0.07	0.084	0.07	−0.075	0
Leaf blade	Compound	2.26	5.5	0.034	−0.14*	**0.188****	0.089
	Entire	0.27	0.66	−0.034	0.14*	**−0.188****	−0.089
Leaf consistency	Hard mesomorphic	1.34	1.9	−0.093	−0.127	0.117	0.067
	Soft mesomorphic	0.92	0.94	0.117	0.138*	−0.114	−0.056
	Scleromorphic	0.52	0.87	0.005	0.037	−0.062	−0.001
	Sub-succulent	0.32	0.83	0.017	−0.051	0.053	−0.029
	Leathery	1.71	0.49	−0.135*	−0.06	0.037	0
Flower position	Not exposed	1.27	1.12	−0.109	−0.041	0.073	0.069
	Exposed	0.29	0.26	0.109	0.041	−0.073	−0.069
Dispersal	Anemochorous	2.26	3.82	−0.02	0.225***	**−0.196****	0.073
	Endozoochorous	2.85	3.5	−0.103	−0.181**	**0.145***	0.061
	Exozoochorous	1.8	3.07	0.072	−0.162*	**0.143***	−0.049
	Autochorous	0.45	0.52	0.019	−0.014	0.017	−0.067
Clonality	Below-ground	2.7	4.14	−0.001	0.234***	**−0.189***	0.018
	None	1.64	3.32	0.087	−0.221**	**0.236****	0.004
	Above-ground	2.04	1.31	−0.11	0.028	−0.096	−0.025

Significance codes: $*P < 0.05$; $**P < 0.01$; $***P = 0.001$.
Traits/attributes significantly correlated with partial RLQ axes are shown in bold. Quantitative traits and attributes within categories are ordered according to their contribution to total inertia of the partial RLQ.

	Axis 1	Axis 2
Life cycle	■	
Growth form		
Habit		
Stem leaf ratio		
Blade fragmentation	■	
Leaf consistency		
Hairiness		
Spinescence		
Wax		
Flower position		
Dispersal mode	■	
Clonality	■	

Fig. 3. Schematic representation of the relationship between whole categorical traits and the first two axes of the partial RLQ resulting from the fourth-corner analysis. Black cells indicate significant associations of traits and axes. The significance of the association between a categorical trait and one axis of the partial RLQ (calculated as pseudo-F, see Dray & Legendre 2008) was combined from two-fourth-corner objects and compared at $\alpha = 0.05$ (for further explanations: see Methods).

watering points were found by Smet & Ward (2005) in semi-arid rangelands of South Africa. These authors observed that pH, resistance (conductivity) and soil nutrients (P, N, organic C) were influential up to a distance of 100 m from watering points through grazing, trampling, defecation and urination. Similarly, our results showed that N and P (NH_4/NO_3 and PO_4 in our case) were significantly elevated with increasing grazing pressure. However, in our analysis these parameters were less relevant in terms of constituting the grazing gradient. Smet & Ward (2006) argue that in the vicinity of watering points, differences in soil nutrients between differently managed farms may occur, caused by altered amounts of mineral supplements given to livestock. In our partial analysis, by removing the effects of habitat differences, the importance of some soil nutrients (e.g. NH_4, PO_4, see Table 5) might have been reduced because the different habitats to some extent also represented differently managed farms.

Plant trait responses to grazing in semi-arid Namibian rangelands

The 'grazing axis' revealed by the partial RLQ represents a complex vector mainly combining processes associated with livestock activities. Hence, this axis characterizes the level of environmental filtering that is relevant for grazing-related plant traits in the studied system.

Important traits and attributes that in the partial RLQ indicate low grazing pressure, are associated with the perennial grass trait group. Although attributes like peren-

nial life cycle, entire leaf blade or leafy stems are also characteristic of other plants besides grasses, this pattern of trait distribution indicates the existence of a fairly homogeneous functional group. Surprisingly, the attribute grass/sedge was of minor importance in the partial RLQ and showed no significant correlation with the first axis. Accordingly, Diaz et al. (2007) concluded that 'graminoid' as an attribute is too general and neglects the different strategy types within this growth form.

The decrease of clonal (rhizomatous) species with increasing grazing pressure in our gradients is in line with the observations of Hoshino et al. (2009) in Mongolia. In contrast, Yeaton & Flores (2009) observed a replacement of tufted grasses by clonal grasses in the southern Chihuahuan Desert grassland at higher grazing intensities. Also, Diaz et al. (2007) reported a positive response of clonal (stoloniferous) grasses to grazing as a globally significant trend. However, the authors stated that this result was mainly influenced by humid systems with a long grazing history. The relatively long history of grazing in our study region is most likely the explanation for differing results in the Chihuahuan Desert (short grazing history) or for similar results in Mongolia (long grazing history). Moreover, there was no complete grazing exclusion, even at the low grazing intensity ends of our gradients, i.e. the gradients might have been too short to reveal a replacement of clonal by tufted perennial grasses. Even relatively low levels of grazing intensity can influence the spatial heterogeneity of vegetation patterns, which in turn may play a significant role in the degree of presence of clonal traits (Benot et al. 2011). We also observed plasticity in growth form among certain grass species, such that clonality was facultative. In undisturbed conditions, these grasses would most likely grow as tufted bunchgrasses, but when grazed they have the ability to produce lateral spread, either above or below the ground. A morphological capacity to change the colonizing strategy under different grazing regimes was proven for grasses in Western Europe (Amiaud et al. 2008), but was also reported for dominant grass species of the arid Patagonian steppe (Adler et al. 2004). The observation that some local grass species possess such plasticity, i.e. the opportunistic activation of growth points after damage, might indicate adaptation to the interactive effects of a long grazing history and the semi-arid climate of the studied system. In this regard, we refer to Milchunas et al. (1988), stating that in semi-arid systems it may be difficult to assess the origin of adaptive trait values since adaptations to aridity may also promote tolerance or avoidance of grazing.

Among continuous traits, we found leaf traits were particularly responsive along the grazing gradients, as shown by a decrease in leaf length/width ratio and an increase in SLA with increasing grazing pressure. This change is asso-

ciated with the decreasing dominance of perennial grasses with tough, narrow leaves in favour of herbaceous forbs with wide and tender leaves. It represents the trade-off between plants with dense leaf tissues, high leaf dry matter content and low growth rates and, in contrast, plants with a high capacity to capture resources, high photosynthetic rates and high growth rates. These two functional strategies correspond to the 'primary axis of adaptive specialization' of species along gradients of resource availability described by Grime et al. (1997), with the first type being favoured in low-productive and the second in high-productive (resource rich) environments. As described in the previous section, the sampled piospheres to some extent also represented gradients in soil nutrient resources. However, results from other studies are in line with our findings that high SLA species with tender leaves, short leaf life span and high growth rates, indicating a grazing tolerance strategy, are favoured under high grazing pressure (Cingolani et al. 2005; Golodets et al. 2009). Altogether, for the gradients sampled, we cannot resolve whether SLA and correlated traits are more indicative of the variation in mineral soil resources or variations in grazing pressure. We rather emphasize the complexity of such gradients and the resulting need to look at trait syndromes instead of single traits when interpreting their grazing responses. Different grazing management schemes add to the environmental complexity and may influence the grazing response (Westoby 1999). While high, continuous stocking promotes a grazing tolerance strategy (high growth rates, high SLA, etc.), under low continuous stocking, allowing for selective grazing, less attractive plants with low SLA, low N content and more fibre can also show a positive grazing response.

High SLA values, in combination with herbaceous growth form, annual life cycle, prostrate–creeping habit, absence of clonal growth, compound leaves and either exo- or endozoochorous dispersal, characterize the plant functional type at the high grazing pressure end of the sampled gradients. This grazing increaser trait syndrome represents a strategy type that captures resources and reproduces quickly by seeds and invests in photosynthetic tissue rather than in stem structures and vertical growth, particularly if there is no horizontal space limitation from competitors.

A low stature (prostrate–creeping habit) can also be regarded as a strategy of grazing avoidance. However, the advantages of low canopy height with respect to grazing avoidance are limited in semi-arid environments that are characterized by a high proportion of bare ground. Under these conditions, taller plants, usually grazing decreasers, do not necessarily receive more attention from grazers (Vesk et al. 2004). In accordance with this statement, plant height showed no significant grazing response along our gradients. Also, Diaz et al. (2007) described a

weak grazing response of canopy height in dry climates, while in their global data set, also including (sub-) humid sites, short plants were more markedly related to high grazing pressure. In contrast to our results, other studies from semi-arid rangelands have reported a significant grazing response of plant height (Landsberg et al. 1999; Jauffret & Lavorel 2003). However, the study of Landsberg et al. (1999) was conducted in semi-arid Australian shrublands that are characterized by a relatively short grazing history as a selective force. The Tunisian steppe vegetation cover in the study of Jauffret & Lavorel (2003) was much lower than in our study sites, and mainly consisted of chamaephytes and therophytes. We think that these differences in vegetation patchiness and structure, as well as historical and present grazing regimes, can significantly contribute to inconsistent trait responses in different study regions (see also Vesk et al. 2004). Using an approach of partitioning environmental variation, for instance in meta-analyses across different regions, could nevertheless be a solution to circumvent this problem.

Most of the other attributes characterizing the grazing increaser plant functional type were also reported in other studies to be influenced by altered grazing impact in relation to annual life cycle (de Bello et al. 2005), herbaceous forb growth form (Vesk et al. 2004), prostrate habit (Jauffret & Lavorel 2003; Diaz et al. 2007) and endozoochorous dispersal (Haarmeyer et al. 2010).

Life cycle as a whole categorical trait, as well as perennial and annual life cycle attributes, showed significant grazing responses. Nevertheless, the high importance of annual and perennial life cycle in the basic RLQ (Table 6) also indicated strong responsiveness to temporal variability and habitat differences. In grazing studies, we therefore suggest a cautious use of these attributes, bearing in mind the temporal and spatial arrangement of the sampling units. However, life cycles complete the picture of the trait syndromes detected at both extremes of the grazing gradient.

In summary, the few attributes of the whole set sampled showing significant grazing responses represent ecologically meaningful response types in the context of a long history of grazing by large mammalian herbivores and the semi-arid climate of the study area. These response types, rather than single attributes, may be used as indicators for rangeland condition in the study area, although not all of the attributes belonging to each of the types have to be necessarily present. To a certain extent, the response types could confirm the patterns detected in other grazing studies. However, we were able to prove that environmental filtering of traits occurs at different spatial (and temporal) scales, including sometimes filtering of the same trait at different scales. To test the validity of response types and

contributing attributes at larger scales would thus be an interesting area for future research.

Methodological issues

As shown in the previous sections, the procedure of simply stratifying our samples according to a categorical covariable (habitat-year) and applying a partial RLQ was successful in extracting grazing response traits. This approach may be an option for other studies where a factor can be assigned to structure the samples spatially or temporally. Accordingly, it could be a useful method to account for spatial or temporal autocorrelation in the analysis of trait–environment relationships. However, partial analysis is a general approach that can allow easy consideration of several categorical and/or quantitative covariables.

Due to the significance level used for comparison with the P-value of the combined fourth-corner approach (α was 0.05 instead of square root of 0.05, as proposed in Dray & Legendre 2008), a relatively low number of traits were significantly correlated with the partial RLQ axes (Table 6). This conservative level of hypothesis testing revealed only the most consistent trait responses. The analysis is therefore suited to include many traits inductively, while still ensuring a stable interpretation. With our approach, a pre-selection of traits, as suggested by Bernhardt-Römermann et al. (2008), is not necessary. By focussing on the significant trait responses only, the multivariate aspect of plant functional response is preserved, no subjective criteria need to be introduced, and a robust interpretation is achievable.

Conclusions

In semi-arid environments, trait responses to grazing are often less clear and can depend on local and regional factors, such as grazing management, altered rangeland condition, productivity (rainfall) and the evolutionary history of grazing. In order to obtain robust interpretations in trait-based approaches, methods are needed that reveal consistent trait responses across various environmental settings. Common plant trait approaches may not be sufficient to seek generalities when comparing different environments. One important outcome of our analysis was that the extent of trait responses could vary in samples from different habitats and years, despite a strong grazing gradient common to all these samples. We emphasize the importance of elucidating the individual contributions of different factors to trait variation. Further, we stress the use of inductive trait sampling strategies, which in combination with adequate multivariate methods, preserves the option of fine-grained interpretations. In this context, we point to a cautious interpretation of previously accepted grazing responses

from traits like growth form, plant height or life cycle. We highlight the potential of our approach for comparisons of trait responses at larger geographical scales and for more detailed studies of temporal changes of trait responses in variable environments such as semi-arid rangelands.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Q-table: Matrix of 87 plant species, nine quantitative and 12 categorical traits, recorded in central Namibia. Trait values of quantitative traits are averages of ten full-grown plant individuals.

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