



Functional structure of an arid steppe plant community reveals similarities with Grime's C-S-R theory

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Keywords

Community-weighted mean; Eastern Morocco; Fourth-corner analysis; grazing; Precipitation fluctuation; Trait correlations; Water stress

Abbreviations

LA = leaf area; SLA = specific leaf area; LDMC = leaf dry matter content; LNC = leaf nitrogen content; carbon:nitrogen ratio = C:N; $\delta^{13}\text{C}$ = ^{13}C isotope content; $\delta^{15}\text{N}$ = ^{15}N isotope content; H_{max} = plant maximal height; A_{max} = carbon assimilation; CWM = community-weighted mean; PCA = principal components analysis; RDA = redundancy analysis.

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Abstract

Questions: (1) How do community-weighted mean (CWM) trait values of 23 functional traits measured on 34 plant species vary along a gradient of aridity under grazed and ungrazed conditions in an arid steppe? (2) How does variation in our CWM trait values differ from those of more mesic grasslands?

Location: Eastern Morocco.

Methods: We measured relative abundance and functional traits along a short aridity gradient over two consecutive years at five heavily grazed sites, each with an enclosure preventing grazing. We analysed the relationship between aridity, grazing, and the expression of CWM trait values using ordination methods and a fourth-corner analysis.

Results: Unconstrained and constrained ordinations identified three distinct suites of temporally consistent functional traits that co-varied with aridity and grazing, and the fourth-corner analysis identified a number of significant but weak trait–environment associations. Grazing selected for short, fast-growing annual species with high SLA, high pastoral value and low seed mass, while aridity selected for species possessing succulent leaves with high $\delta^{13}\text{C}$ leaf content, spines, low LDMC and short stature, although the relative importance of precipitation and grazing changed between years.

Conclusions: Although distinct from more mesic grasslands, our study sites exhibited patterns of trait correlations that were similar to the worldwide leaf economics spectrum. These correlation patterns represented three groups that were reminiscent of Grime's C-S-R model. Direct ordinations supported this interpretation. Temporal variation in our results was due in part to precipitation fluctuations. Our results also indicated selection for a grazing avoidance strategy under heavy grazing. Integrating plant functional traits in conservation and management of arid ecosystems represents a novel and challenging task to ensure more sustainable use of these lands.

Introduction

Arid rangelands, which cover approximately 25% of the world's land area, support nearly 20 million households (Blench 2001), and are of vital economic importance for nomadic and sedentary pastoralists in developing countries (Narjisse 2000; Hatfield & Davies 2006; Lund 2007). However, these ecosystems are at risk of irremediable degradation and desertification because of erratic and low precipitation regimes, soil erosion and increasing grazing

pressure (Sombroek & Sene 1993). These ecosystems are rarely privately owned and, thus, subject to the 'Tragedy of the Commons' (Hardin 1968). Therefore, there is a serious need to maintain their ecological integrity.

To preserve and manage arid rangelands, we must understand how their plant communities are influenced by the two major environmental gradients structuring these ecosystems, namely water availability and grazing intensity, and how such communities might differ from those of better-known mesic grasslands. It is becoming

clear that major ecosystem properties are determined more by functional than by taxonomic properties of vegetation (Díaz & Cabido 2001; Díaz et al. 2007a). Plant functional traits have proven useful in understanding the impacts of grazing and aridity on plant community structure (Jauffret & Lavorel 2003; de Bello et al. 2006; Zheng et al. 2009). Changes in plant community functional structure translate into modification of ecosystem functioning and services in grasslands (Díaz & Cabido 2001 and references therein). An important impact of grazing on ecosystem functioning in grasslands is the change in plant functional groups leading to a reduction of above-ground net primary production (Rusch & Oesterheld 1997). Also, altering the plant community structure can lead to a change in drought resistance (Symstad & Tilman 2001). Assessing the significance of grazing in arid grasslands is thus of primary importance for the understanding of plant community assembly and its effect on ecosystem functioning. In this paper, we describe how a suite of 23 functional plant traits varies along these two key environmental gradients in the eastern Moroccan steppes.

In contrast to more mesic rangelands, little research has been conducted on the functional traits that are most important in arid rangelands and how average values of such traits change along environmental gradients. In fact, these ecosystems are among the most under-represented in global trait databases such as TRY (Kattge et al. 2011). The most exhaustive work on functional variation in rangelands is a meta-analysis by Díaz et al. (2007b), who compiled data from 197 studies of plant trait responses to grazing from across the globe. Although these authors identified some tendencies of plant traits in response to grazing (i.e. short, annual species with a prostrate habit), these trends were usually less clear in arid ecosystems with a long history of grazing. A clear result, however, was that palatability tended to decrease in arid systems with a long history of grazing (Díaz et al. 2007b).

Several plant community studies in arid rangelands have reported changes in plant functional types with grazing pressure (Jauffret & Lavorel 2003; Adler et al. 2004; Navarro et al. 2006; Anderson & Hoffman 2007; Angassa & Oba 2010), but no common tendencies could be extracted from these studies, except that grazing value (i.e. based on preference of livestock for different plant species) decreased with increased grazing pressure (Jauffret & Lavorel 2003). Furthermore, these studies usually did not include quantitative functional traits such as specific leaf area, plant height and seed mass, which would facilitate comparisons between studies, and that are thought to express fundamental trade-offs controlling plant strategies (Westoby 1998). Responses of these traits to grazing pressure have been documented mostly for temperate and semi-arid ecosystems (e.g. Díaz et al. 2001; Peco et al.

2003; de Bello et al. 2006; Garnier et al. 2007; Zhao et al. 2009; Zheng et al. 2009; Niu et al. 2010).

In a multi-site analysis that did not include arid sites, Garnier et al. (2007) showed that grazing affects community-weighted mean (CWM) values of whole-plant and leaf traits (plant height, specific leaf area, leaf dry matter content, and leaf nitrogen, carbon and phosphorus content). A focus on arid rangelands is important because the ecological strategies employed by plants to deal with grazing might be different from those used in more mesic rangelands (Cingolani et al. 2005). Grime's (1974, 1977, 2001) C-S-R model is perhaps the most empirically rich treatment of plant ecological strategies that are based on functional traits related to stress and disturbance, but it has been based primarily on the British flora, for which the levels of 'stress' associated with aridity are clearly not comparable. Grime's C-S-R model is based on two fundamental selective forces (stress and disturbance) that give rise to three primary strategic extremes: competitor species, stress-tolerant species and ruderal species. Competitor species (C-strategists) are encountered in low stress and low disturbance areas. They have a high growth rate, produce a lot of biomass that is rapidly replaced, are tall and can outcompete other species because they exploit resources efficiently. Stress-tolerant species (S-strategists) are encountered in high stress and low disturbance areas. They have a slow growth rate, a long leaf life span and high rates of nutrient retention. Ruderal species (R-strategists) thrive in low stress and high disturbance areas. They have a high growth rate, complete their life cycle in a short period, can produce large quantities of small seeds and are usually annuals. Grime's C-S-R model has primarily been applied to herbaceous vegetation in the more mesic and productive areas of Britain and Northern Europe (e.g. Hodgson et al. 1999; Grime 2001). It has also been applied with success to vegetation undergoing primary succession following glacier melting in the Italian Alps (Caccianiga et al. 2006) and by Cerabolini et al. (2010) to alpine and Southern European vegetation. The subsequent identification of a fundamental, and very general, trade-off in leaves between resource acquisition and retention (Wright et al. 2004; Shipley et al. 2006) has largely contrasted S-strategists (resource retention) with both R- and C-strategists (resource acquisition).

Our primary objective was to describe how 23 CWM functional traits (Table 1) vary as a function of aridity and as a function of grazing in the arid steppes of eastern Morocco. More specifically, we asked two questions: (1) How do community-weighted mean (CWM) trait values of 23 functional traits measured on 34 plant species vary along a gradient of aridity under grazed and ungrazed conditions in an arid steppe? (2) How does variation in our CWM trait values differ from those of

Table 1. List of functional traits used to describe the functional structure of vegetation along an aridity gradient in grazed and ungrazed conditions. The different traits were chosen to reflect a wide variety of ecological functions.

Functional traits (Abbrev., units)	Variable type	N	Ecological relevance ²
Leaf area ¹ (LA, mm ²)	Continuous	25	Stress avoidance, light acquisition
Specific leaf area ¹ (SLA, mm ² mg ⁻¹)	Continuous	25	Resource acquisition/retention
Leaf dry matter content ¹ (LDMC, mg g ⁻¹)	Continuous	25	Resource acquisition/retention
Leaf nitrogen content ¹ (LNC, mg g ⁻¹)	Continuous	5 pooled samples of 5 individuals each	Resource acquisition/retention, palatability
Carbon:nitrogen ratio ¹ (C:N)	Continuous	5 pooled samples of 5 individuals each	Resource acquisition/retention, decomposition
¹³ C isotope content ¹ ($\delta^{13}C$, ‰)	Continuous	5 pooled samples of 5 individuals each	Stress resistance
¹⁵ N isotope content ¹ ($\delta^{15}N$, ‰)	Continuous	5 pooled samples of 5 individuals each	Potential to fix nitrogen
Maximum plant height (H_{max} , cm)	Continuous	50	Competitive ability
Seed mass (g)	Continuous	5 samples of 20–100 seeds	Dispersal strategy, establishment success
Carbon assimilation (A_{max} , $\mu\text{mol g}^{-1} \text{s}^{-1}$)	Continuous	6	Resource acquisition/retention
Leaf osmotic potential (MPa)	Continuous	3	Stress resistance
Annual life cycle	Binary	–	Stress and disturbance avoidance
Woody stem	Binary	–	Stress and disturbance avoidance
Clonality	Binary	–	Competitive ability
Succulence of leaves or stems	Binary	–	Stress resistance
Presence of spines	Binary	–	Grazing resistance, stress avoidance
Onset of flowering (month)	Ordinal	–	Stress and disturbance avoidance
Pastoral value (on a 1–10 scale)	Ordinal	–	Palatability, productivity
Five seed survival adaptations (Table 4)	Categorical	–	Dispersal strategy, establishment success

¹Traits measured on the same individuals.

²Based on Grime (2001) and Cornelissen et al. (2003) and references therein.

more mesic grasslands? We expected that plant communities would respond to water stress by adopting traits that minimize water losses (e.g. succulent leaves, low osmotic potential, C4 metabolism, small leaf area) and would respond to grazing by adopting grazing resistance traits (e.g. spines, lower palatability, tougher leaves, investment in woody structures).

Methods

Study sites

We conducted this study in the arid steppes of the provinces of Boulemane and Figuig, eastern Morocco (Fig. 1). The land, which is collectively owned, has been degraded due to excessive grazing pressure from sheep and goats, the absence of fallow periods, and the harvesting of woody species (Ait 1996; Msika et al. 1997). For the purpose of this study, we selected five sites (Table 2) along a short precipitation gradient, each having both grazed and ungrazed (slightly grazed in the case of the Lamjalil site) areas. The ungrazed sites were permanent exclosures maintained by the Emirates Center for Wildlife Propagation (ECWP) (Missour, Maatarka, Enjil and Lamjalil sites) and the Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification (Eaux et Forêts) (Tirnest site).

The aridity gradient

The climate in this area has been described as Mediterranean arid, with cold winters and hot dry summers

(Le Houérou 1995). Drought occurs from Jun to Sep. Rainfall episodes are mostly concentrated from Mar to May but a non-negligible proportion is also received in Sep and Oct after the summer droughts. Rainfall can be very variable from 1 yr to the next (Le Houérou 1995).

To better illustrate the fact that our study system was different from the types of grazed grasslands that have been more extensively studied, we have summarized different locations from Western Europe and North Africa, and their respective aridity indices (potential evapotranspiration to rainfall ratio) in Table 3. A higher index indicates a more arid site. Thus, our sites were almost eight to 12 times as arid as those in Sheffield (UK) and almost four to six times as arid as those in Montpellier (France) for Enjil (the least arid of our study sites) and Missour (the most arid of our study sites), respectively.

Meteorological stations that are maintained by the ECWP allowed us to quantify monthly precipitation and mean temperatures for the Missour, Maatarka and Enjil sites. Meteorological data were not available in close proximity to the other sites and so we proceeded as follows. First, we regressed mean values of annual precipitation, monthly minimum and maximum temperatures, and monthly relative humidity that were recorded at the ECWP meteorological stations against values provided by the Climate Information Tool (CIT) on the Food and Agriculture Organisation (FAO) website (<http://www.fao.org/nr/water/aquastat/gis/index3.stmv>) to determine the accuracy of CIT values in our region. Given monthly

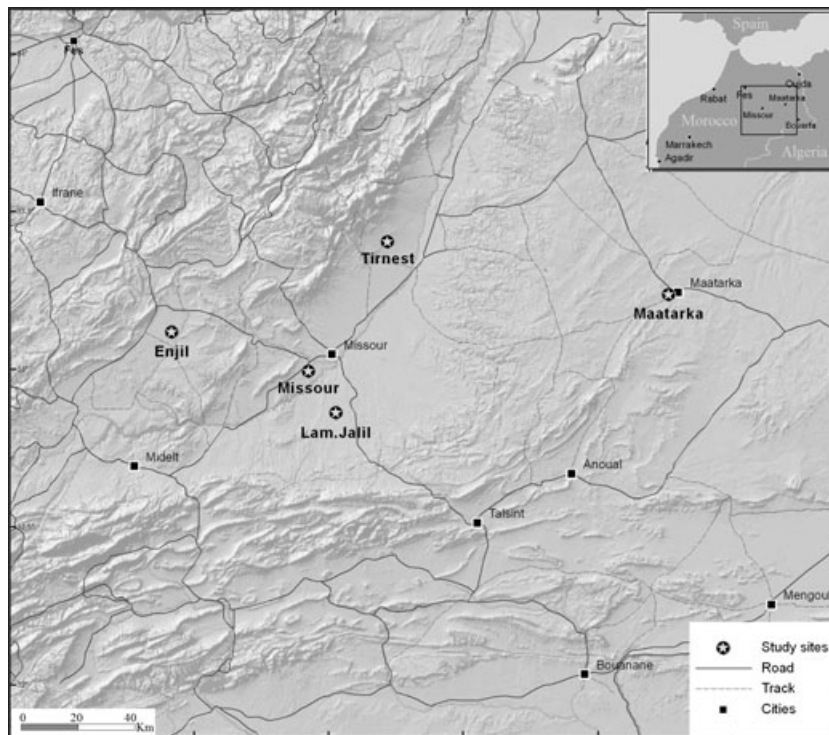


Fig. 1. Locations of the five study sites in eastern Morocco where plant communities were assessed and functional traits measured inside and outside exclosures (50 plots).

Table 2. Environmental variables used to characterize aridity and grazing pressure in the five study sites of eastern Morocco. Precipitation and temperature data for the Missouri, Maatarka and Enjil sites were obtained from local meteorological stations, while those for the Tirnest and Lamjalil sites were estimated by regression equations (see text for further details).

Environmental variables	Sites				
	<i>Missour</i>	<i>Lamjalil</i>	<i>Tirnest</i>	<i>Maatarka</i>	<i>Enjil</i>
	33.006°N	32.894°N	33.414°N	33.257°N	33.160°N
	4.102°W	3.957°W	3.788°W	2.724°W	4.586°W
Annual precipitation (P) (mm)	164	164	190	183	264
Potential evapotranspiration (PET) ¹ (mm)	1546.4	1546.0	1512.6	1492.9	1406.4
Altitude (m)	960	1000	980	1300	1600
Mean maximum annual temperature (°C)	24.1	23.1	24.4	22.6	20.1
Mean minimal annual temperature (°C)	10.7	9.7	11.2	9.3	6.6
Peak of standing biomass	April	April	April	April/May	May
Fenced since	1996	Not fenced ²	1998	2008	2004
Aridity index (PET/P)	9.410	9.432	7.976	8.151	5.331

¹PET is computed with data from the Climate Information Tool (CIT) and adjusted with meteorological data from ECWP weather stations. (<http://www.fao.org/nr/water/aquastat/gis/index3.stmv>).

²The Lamjalil site was not fenced at the time of sampling but see text for further details concerning its grazing history.

values of precipitation, temperature, relative humidity and wind speed, CIT computes monthly and annual evapotranspiration, based on the equations in Allen et al. (1998). This produced strong correlations between ECWP meteorological data and CIT for annual precipitations ($R^2_{\text{adjusted}} = 0.78$, $P = 0.005$), monthly minimum temperature ($R^2_{\text{adjusted}} = 0.98$, $P < 0.001$), monthly maximum

temperature ($R^2_{\text{adjusted}} = 0.96$, $P < 0.001$) and monthly relative humidity ($R^2_{\text{adjusted}} = 0.75$, $P < 0.001$). Second, we regressed the evapotranspiration values estimated by CIT after imputing the meteorological data from the ECWP against CIT-generated evapotranspiration values when only geographic co-ordinates and elevation were specified. Again, the correlation was strong ($R^2_{\text{adjusted}} = 0.93$,

Table 3. Aridity indices for various locations in Western Europe and North Africa compared with two of our study sites (Enjil and Missouri).

Location	Aridity index ¹
Sheffield, UK	0.706
Amsterdam, Netherlands	0.756
Edinburgh, UK	0.818
Paris, France	1.133
Montpellier, France	1.416
Córdoba, Spain	2.490
Madrid, Spain	2.758
Enjil, Morocco ²	5.331
Missour, Morocco ²	9.410
Bouarfa, Morocco ³	14.651

¹The aridity index is computed with data from the Climate Information Tool (CIT).

(<http://www.fao.org/nr/water/aquastat/gis/index3.stmv>).

²Indices for these sites were adjusted with meteorological data from ECWP weather stations.

³Bouarfa is a city located relatively close to the Sahara Desert.

$P < 0.001$). This allowed us to compute valid aridity indices (evapotranspiration:rainfall ratios) for all sites.

Water availability was superior in 2009, with higher than normal precipitation prior to the growing season during autumn of 2008 (410 mm in Sep and Oct 2008), while conditions were more similar in 2010 to long-term average values (81 mm in Sep and Oct 2009) (Fig. 2), albeit slightly more humid.

Grazing enclosures

The intensity of grazing by sheep and goats in our study sites was divided into two classes: intense grazing wherever grazing was permitted, or its absence wherever grazing was prevented. Land use for grazing is year-round and average stocking rates are estimated to be around 1.6 animal unit $\text{ha}^{-1} \text{yr}^{-1}$ (Laouina et al. 2001). Steppes can provide as much as 75% of herd fodder requirements during wet years but this amount can drop to 30% during dry years (Lazarev 2008). Each site was fenced at a different time, thus creating a temporal gradient of vegetation response after grazing was prevented (Table 2). For the Missouri, Maatarka and Enjil sites, no grazing was allowed after a fence was constructed. The Tirnest site had an enclosure for about 30 gazelle from 1998 to 2003 and was kept ungrazed thereafter (Eaux et Forêts, pers. comm.). The Lamjalil site possibly had a grazing history that was different from the other sites. It had been fenced at the end of the 1950s and was used for agronomic and pastoralist experiments by the Institut National de la Recherche Agronomique (INRA, France), with densities of about one sheep ha^{-1} (Direction Provinciale de l'Agriculture, pers. comm.). After 2004, the fence was removed and the site

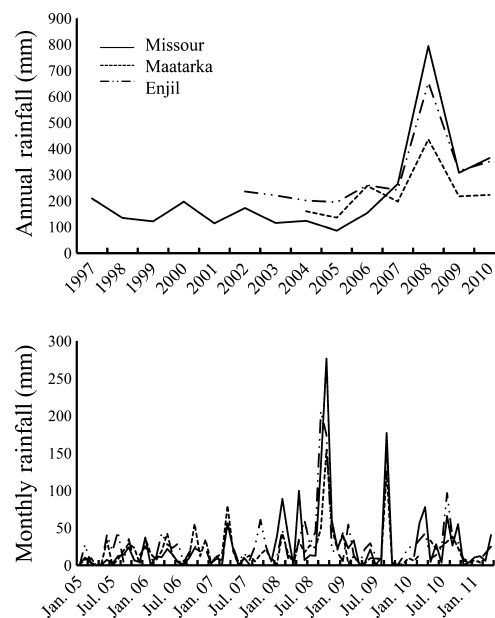


Fig. 2. Annual and monthly rainfall (in mm) for the Missouri, Maatarka and Enjil sites. Data were recorded by meteorological stations maintained by the Emirates Center for Wildlife Propagation. The peak in 2008 is due to unusually high levels of precipitations in Sep and Oct of the same year.

remained loosely protected by two guards to limit grazing pressure, although it is likely that moderate grazing still occurred. Another fence was put up by the ECWP during summer 2010.

Determination of community structure

For each of the five sites, we randomly located ten plots within steppe vegetation to measure species abundance and functional traits, while avoiding heterogeneous areas like wadis, drainage lines and flooding surfaces (*sensu* Le Cuziat 2005). We sampled five plots in grazed conditions and five plots in ungrazed conditions (i.e. within enclosures). The plots were separated by at least 800 m in grazed conditions and 500 m in ungrazed conditions to avoid pseudo-replication (Hurlbert 1984).

We assessed species abundance based on plant cover within each of the 50 plots using the point-intercept method (Daget & Poissonnet 1971) in 2009 and 2010. The same plots were sampled in both years. We preferred a transect-based method rather than a quadrat-based method to estimate plant cover because most grazed sites had very low and sparse vegetation cover and would have required intensive sampling effort when using quadrats. The point-intercept method based on plant cover yields essentially the same results for CWM trait values (Lavorel et al. 2008) or species abundances for annual grasses and perennial forbs (Chiarucci et al.

1999) as when biomass is used. Briefly, we recorded species presence along 20-m long transects by lowering a thin dowel every 10 cm. We noted every individual in contact with the dowel, and multiple contacts were possible for an individual at each point. A minimum of three parallel transects, which were separated by 6 m, were established within each plot. If a minimum of 100 intercepts with vegetation was not attained, extra transects were sampled until that number was reached to obtain an appropriate estimate of community structure (Daget & Poissonnet 1971). We calculated species relative abundance by dividing the number of contacts for each species by the total number of contacts in each plot. Species that accounted for 85% of total community abundance were selected for trait measurements because this value constitutes a reasonable compromise between accuracy and sampling effort (Pakeman & Queded 2007).

Trait selection and measurements

Based on literature searches, we selected 23 functional traits targeted for their potential to respond to aridity and grazing gradients (Table 1). The various seed survival adaptations that we considered, together with a brief description, are listed in Table 4.

Leaves that were used for leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC) measurements were sampled and treated following Garnier et al. (2001b). The leaf samples were directly placed in vials filled with deionized water at the moment of harvest, transported in a cooler box back to the laboratory as soon as possible, and stored for about 18 h at 4 °C. Leaf saturated mass was weighed to the nearest 0.1 mg and leaf area (mm²) was obtained with ImageJ software (version

1.41; NIH, Bethesda, MD, USA). Leaves were then oven-dried at 60 °C for 72 h. To minimize measurement errors, leaf masses and areas were always measured by the same individual. Dried leaves were further processed for leaf nitrogen content (LNC), carbon:nitrogen ratio (C:N), ¹³C isotope content (δ¹³C) and ¹⁵N isotope content (δ¹⁵N). LNC and C:N were measured using an elemental analyser (ANCA-GSL; SerCon, Cheshire, UK). Isotope values for ¹³C and ¹⁵N were determined by continuous flow isotope ratio mass spectrometry at the Stable Isotope Facility of the University of California-Davis.

Plant reproductive height (H_{max}) and seed mass were measured following Cornelissen et al. (2003). Seed dry mass was obtained by weighing five groups of dried seeds (up to 100 seeds for very small seeds) each originating from ten individuals. Before drying and weighing, seed viability was visually assessed and seeds showing signs of parasitism were removed. We used seed mass data provided by Kew Royal Botanic Gardens (<http://data.kew.org/sid/>) for *Noaea mucronata* (Forssk., Asch. & Schweinf), *Stipagrostis ciliata* (Desf., De Winter), *Koelipinia linearis* (Pallas) and *Filago pyramidata* (L.) because insufficient quantities of their seeds were harvested in the field. Mass-based carbon assimilation (A_{max} ; μmol mg⁻¹ s⁻¹) was measured with an open-path, portable photosynthesis system (Model LI-6400-XT; Li-Cor Biosciences, Lincoln, NE, USA). Leaf osmotic potential was measured using the hot water extraction method followed by freezing point osmometry (Osmette II; Precision Systems, Natick, MA, USA) (Callister et al. 2006).

Categorical trait information (plant life form, clonality, presence of succulence and spines, onset of flowering, specific index of pastoral value and seed survival adaptations) were obtained from local floras and from direct observations of botanists. The specific index of pastoral value is an integrative index of palatability that is used by agronomists to judge the quality of pastures and rangelands (Akpo et al. 2002) and based on a combination of productivity and nutrient content.

All traits were measured in April and May at the peak of standing biomass when most species sampled had reached the reproductive stage (except for Chenopodiaceae which flower in the autumn). Because of the short sampling period available, we measured LA, SLA, LDMC, LNC, C:N, δ¹³C, δ¹⁵N, H_{max} and seed mass from individuals sampled during the 2009 field season. A_{max} and leaf osmotic potential were measured from individuals sampled during the 2010 field season. This implies that, for each trait, we assigned a single value per species. Although there is certainly some variation at the intra-specific level (Albert et al. 2010), the ranking of single traits among species should be relatively constant between years (Garnier et al. 2001a).

Table 4. Brief description of seed survival adaptations to environmental conditions.

Seed survival adaptation	Description ¹
Bradyspory	Dispersal of diaspores from the mother plant is delayed and spread over significant periods of time
Hygrochasy	Opening of the dispersal unit (or organ of the mother plant enclosing the dispersal units) as a function of moisture (i.e. opening when wet)
Myxospermy	An anchorage mechanism, where mucilage is produced upon being moistened
Synaptospermy	Two or more seeds (or one-seeded fruits) are joined together to form a compound diaspore
Trypanocarpy	The form and/or appendages of the diaspore favour burial in the soil at the point of initial contact (e.g. by drilling or wedging into cracks)

¹Based on Gutterman (1993).

Statistical analysis

Trait data were first analysed with principal components analysis (PCA) to visualize patterns of correlation among traits at the community level. To do so, we used a matrix containing the CWM values for each plot. We computed CWM values following Garnier et al. (2004). Although some of the functional traits that we considered are categorical variables, it is acceptable to use PCA, because multiplication of these values by the species' relative abundances converts them into continuous variables. This is equivalent to classic ordination analyses where species relative abundances are used. CWM data were centred and standardized to give equal weight to the different traits.

Redundancy analysis (RDA; a constrained linear ordination technique: Lepš & Smilauer 2003) was performed with the matrix containing CWM trait values for each plot and another matrix containing two environmental variables: time since enclosure and aridity index (Table 2). We chose a linear ordination rather than a unimodal ordination method based on the criteria of Lepš & Smilauer (2003) but also because trait–environment relationships should be linear or monotonic at least over short environmental gradients (Garnier et al. 2004; Cingolani et al. 2007). All CWM values were centred and standardized before analysis to give equal weight to all traits. Ordinations were performed using the *vegan* package available within the R statistical environment (R Development Core Team, Vienna, Austria).

To assess the significance of each of the environmental variables on trait values, we performed a fourth-corner analysis (Legendre et al. 1997; Dray & Legendre 2008). This allowed a direct, simultaneous comparison of three matrices containing information on species abundances, species functional traits and environmental variables. We chose permutation model #2 (the 'species assemblage' model (*sensu* Dray & Legendre 2008): permutation of the rows of the plots per species matrix) with 9999 permutations. This created a null model representing the case where 'species assemblages were randomly attributed to sites, irrespective of the site characteristics' (Dray & Legendre 2008). This null model preserves both the link between species and their traits and the pattern of trait co-variation. Holm's correction for multiple testing was used to limit the inflation of Type-I errors (Holm 1979). The fourth-corner analysis provided a multivariate statistic (S_{RLQ}) that tested the global link between the trait matrix and the environmental variables and a statistic (r , F or χ^2 , depending on the nature of variables) for each trait–environment combination (Dray & Legendre 2008). Fourth-corner analyses were performed using the *ade4* package available within the R statistical environment (R Development Core Team).

Because we had different durations of enclosure at the various aridity levels, these two environmental variables were not uncorrelated. To correct for this, we regressed the duration of enclosure against aridity and vice versa, and used the residuals of each dependent variable (aridity or duration of enclosure) as the input for the fourth-corner analysis. The relationship between duration of enclosure and aridity was positive and non-negligible ($r^2 = 0.28$, $P = 0.007$), because the enclosures with the longest length of enclosure were located in the more arid sites. By considering only the residuals, we statistically controlled for the problem of co-variation between duration of enclosure and aridity.

Results

Trait correlations and response to environmental conditions

The first and second axes of PCA, based on CWM traits, explained, respectively, 33.8% and 22.3% of total variance in 2009, and 33.2% and 25.1% in 2010. The CWM plot values for all functional traits are included as supplementary material in App. S1. Results from the PCA analysis identified three distinct groups of trait correlations (Fig. 3). The first group of such trait correlations corresponded to communities dominated by species that have high values of plant height, seed mass, LDMC and C:N ratio, and which show clonality. The second group represented communities that are composed of woody shrubs with high values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which possess succulent leaves or stems, spines and low leaf area, and that flower after water stress. The third group consisted of communities with high specific pastoral values, LNC and SLA values, annual life cycle, low seed mass and high (less negative) osmotic potential. Although both years had roughly the same correlation patterns, axis 1 on the 2009 PCA graph was associated with the third group, while axis 1 in 2010 was associated with the second group.

RDA showed how community functional structure responded to environmental conditions (Fig. 4). The first and second axes respectively explained 11.8% and 6.5% of total variance in 2009 and 11.5% and 6.6% in 2010. In 2009, as aridity increased, CWM trait values tended to decrease for specific pastoral value, seed mass, LDMC and plant height, while CWM trait values tended to increase for succulence, spinescence, $\delta^{13}\text{C}$, annual life form and LNC. Along the second axis, longer time without grazing induced a shift towards communities with high LDMC, low SLA, a high proportion of woody shrubs, late onset of flowering, high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and low pastoral value. In heavily grazed conditions, communities were likely to be composed of annual species with high SLA, LNC and specific pastoral values.

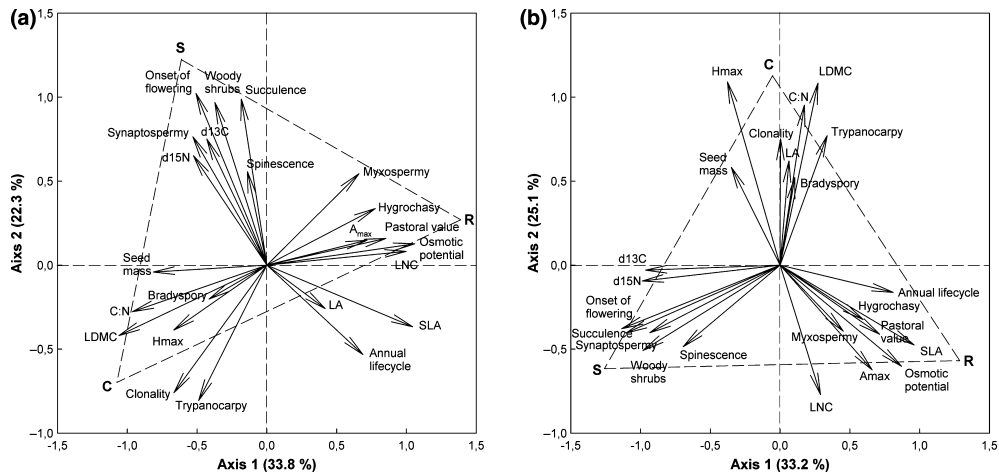


Fig. 3. Ordination plots of the CWM trait matrix with abundance data from (a) 2009 and (b) 2010 resulting from principal components analysis. Axes 1 and 2 explain 33.8% and 22.3% of variance, respectively, in 2009 and 33.2% and 25.1%, respectively, in 2010. Grime's C-S-R triangle was added to the plots to display the three primary strategic extremes. Acronyms are listed in Table 1.

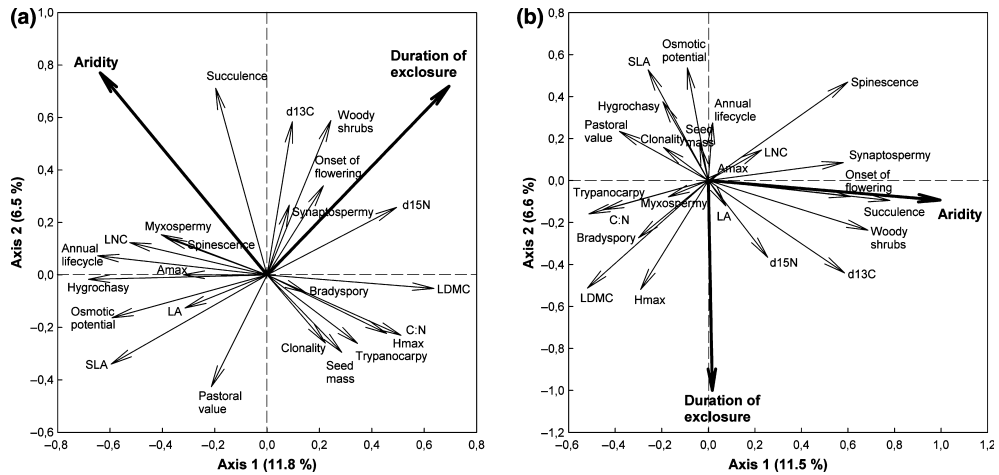


Fig. 4. Ordination plots of the CWM trait matrix with abundance data from (a) 2009 and (b) 2010 resulting from redundancy analysis with aridity and duration of exclusion as environmental variables. Axes 1 and 2 explain 11.8% and 6.5% of total variance, respectively, in 2009 and 11.5% and 6.6%, respectively, in 2010. Grime's C-S-R triangle was added to the plots to display the three primary strategic extremes. Acronyms are listed in Table 1.

In 2010, similar trait responses to the environment were observed, but aridity was closely associated with PCA axis 1, and duration of exclusion with axis 2. A major difference in 2010 was that the annual life form was not associated with aridity but rather with duration of exclusion. Also, LDMC and plant height were more correlated to the duration of exclusion than in 2009.

Formal testing of trait–environment relationships: the fourth-corner analysis

The multivariate S_{RLQ} statistic indicated a significant relationship between the trait matrix and the environmental variables for 2009 ($S_{RLQ} = 0.976, P < 0.001$) and 2010

($S_{RLQ} = 1.425, P < 0.001$). For 2009, plots with a longer duration of exclusion were associated with low LA and SLA, high $\delta^{13}C$ and $\delta^{15}N$, an increase in woody shrubs and succulent leaves, later onset of flowering and synaptospermy as an adaptation to seed survival (Table 4). In 2009, aridity favoured low LDMC and C:N ratios, high LNC, species with short stature and low seed mass, an annual life form, spinescence, succulence and myxospermy and hydrochasy as an adaptation to seed survival.

In 2010, fourth-corner results exhibited some noticeable differences from those obtained for 2009 (Table 5). For example, in 2009, aridity seemed to favour an annual life form, but in 2010, woody shrubs were positively correlated with aridity. Aridity was also positively correlated with

$\delta^{13}\text{C}$ in 2010, but this relationship was not significant in 2009. Onset of flowering responded only to aridity in 2010, but only responded to duration of enclosure in 2009.

The traits that showed the greatest consistency (i.e. same response for both years) with aridity are LDMC, C:N ratio, H_{max} , spinescence, succulence and trypanocarpy. The duration of enclosure was significantly associated with SLA, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and osmotic potential for both years. Some traits did not show any significant relationship for either environmental variable. In 2009, the associations of aridity or duration of enclosure with pastoral value and brady-spory were not significant. In 2010, the associations of aridity or duration of enclosure with LA, LNC, seed mass, and annual life form were not significant. There was no significant association between aridity and either duration of enclosure with clonality and A_{max} in either year.

Discussion

How do CWM trait values co-vary along the aridity and grazing gradients?

Although the C-S-R model has been overwhelmingly applied to species-level patterns of trait correlation, Grime's (1974) original paper also applied it to community-level patterns via abundance weighting. This study is one of the few extensions to community-level patterns of trait correlation. Moreover, it is also one of the few studies to examine such trait correlations in vegetation that is experiencing both extreme environmental stresses due to water limitation and extreme disturbance due to overgrazing by sheep and goats. Our enclosure treatments have allowed us to see how the reduction of disturbance for a constant level of stress changed the trait values.

Let us first consider the patterns of trait co-variation without reference to the environmental gradients. The 2009 PCA (Fig. 3a) identified three groups of CWM traits that broadly corresponded to Grime's three primary strategies. The first axis contrasted traits of resource acquisition and retention between R- and C-strategists and represents a community-level equivalent of the worldwide leaf economics spectrum (Wright et al. 2004). Vegetation that loaded positively on the first axis (Fig. 3a) was dominated by plants that can rapidly acquire, but also rapidly lose, resources: an annual life cycle, leaves with high SLA, high osmotic potential, high leaf N and high A_{max} . These traits have often been associated with a high maximum relative growth rate (Poorter & Remkes 1990; Reich et al. 1992) and allow species to grow rapidly and complete their life cycle in a short period. Many of these traits explained why the dominant species in such communities have high pastoral value. We interpreted this strategy as grazing avoidance. This strategy is probably more suitable when a stress is juxtaposed on disturbance. Grazing resistance (by invest-

Table 5. Results of the fourth-corner analysis. This analysis indicates the tendency of the permutation results for each significant trait–environment combination. For significant relationships at the 5% significance level, the sign indicates if the observed value is above (+) or below (–) the expected value (mean of the permutation results).

Traits	Aridity		Enclosure	
	2009	2010	2009	2010
LA	n.s.	n.s.	–	n.s.
<i>r</i>			–0.142	
SLA	n.s.	n.s.	–	–
<i>r</i>			–0.227	–0.217
LDMC	–	–	n.s.	+
<i>r</i>	–0.244	–0.290		0.202
$\delta^{13}\text{C}$	n.s.	+	+	+
<i>r</i>		0.253	0.213	0.276
$\delta^{15}\text{N}$	n.s.	n.s.	+	+
<i>r</i>			0.229	0.265
N	+	n.s.	n.s.	n.s.
<i>r</i>	0.167			
C:N	–	–	n.s.	n.s.
<i>r</i>	–0.227	–0.188		
H_{max}	–	–	n.s.	+
<i>r</i>	–0.205	–0.176		0.219
Seed Mass	–	n.s.	n.s.	n.s.
<i>r</i>	–0.141			
Annual Life Cycle	+	n.s.	n.s.	n.s.
<i>F</i>	2.867			
Woody Stem	n.s.	+	+	n.s.
<i>F</i>		5.870	1.735	
Clonality	n.s.	n.s.	n.s.	n.s.
<i>F</i>				
Spinescence	+	+	n.s.	–
<i>F</i>	0.761	6.049		2.905
Succulence	+	+	+	n.s.
<i>F</i>	2.050	9.819	1.268	
Onset of Flowering	n.s.	+	+	n.s.
<i>r</i>		0.246	0.1396	
Pastoral Value	n.s.	–	n.s.	n.s.
<i>r</i>		–0.196		
Myxospermy	+	n.s.	n.s.	n.s.
<i>F</i>	1.795			
Brady-spory	n.s.	–	n.s.	+
<i>F</i>		1.283		1.584
Synaptospermy	n.s.	+	+	n.s.
<i>F</i>		2.294	0.674	
Hygrochasy	+	n.s.	–	n.s.
<i>F</i>	2.704		1.594	
Trypanocarpy	–	–	n.s.	n.s.
<i>F</i>	1.584	2.472		
Osmotic Potential	+	n.s.	–	–
<i>r</i>	0.159		–0.190	–0.292
A_{max}	n.s.	n.s.	n.s.	n.s.
<i>r</i>				

ment in defensive physical structures and chemical compounds) might have been too costly to be a successful strategy; however, this interpretation needs more empirical support. In our study, spinescence loaded rather

strongly on the second PCA axis, which would indicate that spines were more effective for heat dissipation than for reducing grazing (Aber & Melillo 2001).

Vegetation that loaded negatively on the first PCA axis was dominated by plants that both acquire and lose resources more slowly: clonal perennials (woody or other), leaves with dense tissues and a high C:N ratio but low A_{\max} . Plant height and clonality have usually been assumed to indicate a plant's capacity for competitive dominance (Gaudet & Keddy 1988; Hodgson et al. 1999), but high LDMC and C:N ratio values suggested a retentive strategy of resource capture. The second PCA axis (Fig. 3a) primarily contrasted woody vegetation (positively loading on the second axis) with herbaceous vegetation, and also discriminated vegetation according to traits adapted to reduce water stress or maximize water-use efficiency. Traits like succulent leaves, high $\delta^{13}\text{C}$ leaf content, low SLA and small leaf size are recognized adaptations to resist water stress in hot climates (Farquhar & Richards 1984; Hubick et al. 1986; Aber & Melillo 2001). Late onset of flowering could also be interpreted as a means of avoiding water stress by postponing the flowering stage until after the summer drought (Crimmins et al. 2011). The relative importance of the two axes switched between 2009 (Fig. 3a) and 2010 (Fig. 3b) but without changing the patterns of trait co-variation. This difference probably arose because of the difference in precipitation regime between the 2 yr. The less arid conditions of 2009 might have alleviated the water stress so that the impact of grazing was more noticeable than in 2010.

Using the 2009 ordination (Fig. 3a) as an example, and without reference to the actual environmental gradients, we can therefore recognize Grime's three primary strategies as applied to the community level. A quantitative a priori approach generated similar results, thus confirming our interpretation of the ordination plots (App. S2). Vegetation dominated by R-strategists was found high on axis 1 and low on axis 2. Vegetation dominated by S-strategists was found low on axis 1 and high on axis 2, while C-strategists were intermediate on both axes. Since all our sites were strongly water-limited, and likely nutrient-limited, we would characterize the C-strategists as 'stress-tolerant competitors' (Grime 2001).

Grime's C-S-R theory considers three primary strategies – and various intermediate strategies – but omits the high stress/high disturbance combination because no single species could combine traits that are simultaneously adapted for both extreme stress and extreme disturbance. Although our study was not directly designed to explore this missing combination, it is interesting to note that the grazed plots with the highest water stress (i.e. the Missouri and Lamjalil sites) could correspond to this missing combination. In such plots we observed a combination of traits adapted to

grazing (annual life form, high SLA, low plant height) and to water stress (low osmotic potential, succulence, high $\delta^{13}\text{C}$), although these two combinations of traits did not occur within a single species. Rather, the community consisted of a mixture of more ruderal and more stress-tolerant species. It is therefore possible, in agreement with the C-S-R model, that no single evolutionary solution (i.e. primary strategy) exists for such an environment, but that the community consists of a combination of plants that are all rather poorly adapted for the existing conditions; they are able to occupy the site simply because no superior combination of traits exists.

The RDA results (Fig. 4), in which we constrained the trait ordinations by the measured environmental gradients, provided an independent test of the aforementioned interpretation. In 2010 (Fig. 4b), we observed that the vegetation dominated by R-strategists was indeed associated with the most recently grazed sites (i.e. negatively associated with the duration of exclusion), while the vegetation dominated by C- or S- strategists was more frequently associated with the sites in which grazing had been excluded for longer periods of time. Furthermore, for a fixed duration of exclusion (i.e. grazing exclusion), higher levels of aridity were associated with vegetation that was more strongly dominated by S-strategists. This interpretation was more difficult to achieve for the 2009 results (Fig. 4a) because S-strategists were more strongly associated with the duration of exclusion of grazers, while C-strategists were more strongly associated with lower aridity.

In 2009, RDA results indicated that an annual life cycle is favoured in the sites with increased aridity. This might seem counter-intuitive at first; however, this was not a causal relationship but rather reflected an increased proportion of annuals that accompanied the unusually abundant precipitation in 2009, especially in the more arid sites. In 2010, following much lower levels of precipitation, the annual life cycle was associated instead with the duration of exclusion. The onset of flowering also showed a different response between years, in that it was more related to duration of exclusion in 2009 and to aridity in 2010. Again, this might have been caused by the higher proportion of annuals with an early onset of flowering. This response was consistent with the experiment of Miranda et al. (2009) who showed that altering precipitation input had a strong impact on annual plant community structure. This interpretation was reflected in the environmental variable loadings. In 2009 (Fig. 4a), both environmental variables tended to share roughly the same importance in explaining CWM trait associations with the environment; in 2010 (Fig. 4b), the aridity index was strongly correlated with RDA axis 1 while the duration of exclusion was correlated with RDA axis 2. Again, this suggests that higher

precipitation levels reduced the predominant influence of water stress and, consequently, the impact of grazing was more easily observed than when precipitation levels were lower.

The fourth-corner results (Table 5) also showed that some traits are temporally consistent with aridity (LDMC, C:N ratio, height, spinescence, succulence and trypanocarp) and the duration of exclosure (SLA, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and osmotic potential), while others (e.g. LNC, seed mass, pastoral value, LA, onset of flowering) were only important in some years. Again, we think that this temporal switch occurred because of the difference in precipitation between 2009 and 2010. This switch emphasized that our aridity gradient is quite short (strong water limitation everywhere) and that annual fluctuations are at least as important as the average differences in precipitation in explaining functional plant community structure.

How do arid CWM trait values, and their correlations, differ from those of more mesic grasslands?

Many studies of functional plant community structure in more mesic grasslands have reported patterns of trait correlations, at the species and community levels, across a broad range of stress and disturbance (e.g. Grime et al. 1997; Garnier et al. 2004; Shipley et al. 2005; Gross et al. 2007). Even though the mean and the range of trait values reported differed from those measured in this study (Table 6), it is interesting to note that the trait correlation patterns we observed in arid steppes of eastern Morocco correspond to those previously observed in more mesic grasslands. This reinforces the idea of the existence of a general co-variation pattern in functional traits, regardless of environmental conditions. Trait correlation patterns in this arid ecosystem were no exception to the leaf economic spectrum (Wright et al. 2004; Shipley et al. 2006).

The functional response of vegetation to grazing indicated differences between our study sites and more mesic grasslands. Comparison, however, has not been straightforward, because the high grazing pressure prevalent in

our study sites was probably not comparable to more mesic grasslands having some form of landscape management or control of grazing pressure. Furthermore, grazing in arid ecosystems has usually been performed on marginal lands (Asner et al. 2004) where conventional agriculture is not possible. In arid and semi-arid ecosystems, two broad categories of response to grazing have been reported in the literature: desertification, 'the replacement of herbaceous cover by shrub cover and bare soil', and woody encroachment, 'the addition of woody canopies without major losses of herbaceous cover' (Asner et al. 2004). Grazing has been frequently cited to explain woody encroachment in semi-arid environments (Archer et al. 1995). In more mesic ecosystems, the resource availability model (Coley et al. 1985) and Grime's (2001) C-S-R model should predict investment in photosynthetic tissues to counterbalance the negative impact of grazing on plant growth, whereas investment in anti-herbivore defence should be observed in less productive sites. Based on these theoretical assumptions, we would have expected an increase in woody shrubs and less palatable species with grazing. Rather, we observed the opposite response: an increase in short annual species. Our results are consistent with Milchunas et al.'s (1988) prediction for semi-arid grasslands with a long history of grazing, and reinforces the idea that aridity and grazing are convergent selection pressures (Coughenour 1985). Also, the positive response of shrubs to grazing exclusion is probably due to some dominant shrubs [e.g. *Artemisia herba-alba* (Asso.), *Krascheninnikovia ceratoides* (L.) and various *Salsola* sp.] being heavily grazed outside of exclosures.

Formal testing of trait–environment relationships in observational studies

The inferential statistical conclusions emerging from the fourth-corner analysis largely corroborated the interpretations of the ordination results. Although significant trait–environment associations were found, the strength of these associations was weak: all Pearson's correlation

Table 6. Comparison of functional trait values measured in the steppes of eastern Morocco with other studies from more mesic ecosystems in southern Quebec (Sonnier et al. 2010) and southern France Garnier et al. 2004).

Traits	Species trait range		CWM trait range	
	This study	Sonnier et al. (2010)	This study	Garnier et al. (2004)
SLA ($\text{mm}^2 \text{mg}^{-1}$)	1.91–26.60	5.49–52.87	4.06–17.03	13.0–21.9
LDMC (mg g^{-1})	120–598	100–900	186–478	182–411
H_{max} (cm)	1.8–84.9	10.8–181.1	4.3–56.3	–
LNC (mg g^{-1})	10.9–40.5	10.6–50.7	16.4–31.2	9.5–28.0
LCC (mg g^{-1})	281.3–482.1	353.0–492.9	323.7–456.0	–
Seed mass (mg)	0.01–11.6	0.01–15.3	0.3–2.9	–

coefficients were less than 0.30. One possible explanation might be the length of the gradient considered, since the difference in rainfall between the most and least arid sites was small. Globally, all our sites were strongly water-limited. A second possibility would be the very slow response time of arid ecosystems in response to grazing exclusion. In such extreme environments, exclusion time was probably not long enough to produce clear tendencies in vegetation dynamics (West et al. 1984; Westoby et al. 1989).

A limitation to the use of the fourth-corner method is the way in which environmental variables are measured. In studies with relatively simple environmental gradients, the fourth-corner method is well-suited to answer questions about trait–environment relationships. For example, Aubin et al. (2009) used this method to evaluate the restoration potential of abandoned pastures. Their design consisted of five distinct successional stages, from old-field pastures to mature forest plots. In our case, we had to deal with the pre-existing exclusions, which had protected vegetation from grazing for different lengths of time. The ideal case would have been an experimental design with many exclusions that varied in exclusion duration and were replicated at all precipitation levels. Thus, the impact of exclusion duration on functional traits could have been assessed directly. This is not always technically feasible in observational studies. Because of this, we have had to interpret the results for the ‘duration of exclusion’ variable with caution, not only because the Lamjalil site had a different grazing history to the other sites but also because the exclusions in the more arid sites happened to be the oldest.

Arid ecosystem management from a functional perspective

Despite our initial expectation with respect to sheep grazing, the functional response of the vegetation was not to select for grazing-resistant vegetation, but rather to select for grazing-avoidance vegetation. From an agronomic point of view, pastures should ideally have a high cover of palatable, grazing-tolerant species throughout the year for optimal herding. Indeed, the specific index of pastoral value served as a rough estimate of palatability. The results of the redundancy analysis, especially in 2009, suggested that pastoral value is favoured under grazing. One might erroneously conclude that the present level of grazing should therefore be maintained in the steppes of eastern Morocco, solely based on these results. This is, however, an incomplete assessment of the situation. The traits that were selected under intense grazing in these dry steppes were indeed those that increased the palatability of the vegetation, but these traits were also associated with a short annual life cycle that allows the individual to rapidly

complete its life cycle within a few weeks or a month at most. This means that plant cover will be present for only part of the year, leaving the soil bare for the rest of the year and, therefore, subject to desertification (Le Houérou 1977; Novikoff 1983; Huss 1996; but see Skarpe 2000). Integrating plant functional traits in conservation and management of arid ecosystems represents a novel and challenging task to ensure more sustainable use of these lands.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Community-weighted mean (CWM) values of 23 functional traits measured in the 50 sampled plots (grazed and ungrazed) in eastern Morocco for 2009 and 2010. All CWM values were computed considering plant species representing at least 85% of total community abundance. Trait units and abbreviations are defined in Table 1 of the main paper.

Appendix S2. Additional information concerning the comparison of ordinations based on functional traits and an a priori C-S-R index.

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Graphical Abstract

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We assessed the impact of grazing and aridity on plant communities in arid steppes of eastern Morocco by measuring plant functional traits. We found patterns of trait correlations that are similar to the worldwide leaf economics spectrum and these patterns were related to Grime's C-S-R model. Our results also indicated that grazing avoidance was the strategy favoured under heavy grazing.