

## Assessment of grazing effect on sheep fescue (*Festuca valesiaca*) dominated steppe rangelands, in the semi-arid Central Anatolian region of Turkey

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### ABSTRACT

In the semi-arid steppe rangelands of Central Turkey, *Festuca valesiaca* and *Thymus sipyleus* ssp *rosulans* have become the dominant species on degraded pastures. We hypothesized that decreases in species richness and abundance are correlated with increasing prevalence of these two species. Therefore, our objectives were to determine whether there are patterns in examined vegetation; how dominant species contribute to these patterns; and how patterns differ between grazed and ungrazed vegetation. We determined that protection from grazing increased species richness. Grazing significantly changed composition through decreasing total plant, forb, grass and *F. valesiaca* covers, while substantially increasing *T. sipyleus* cover. Topography, soil and grazing appear to impact the dominance of plant communities where *F. valesiaca* and *T. sipyleus* prevail. These two dominant species had a significant effect in shaping vegetation patterns. Based on regression analysis, alterations in species richness with changes in cover of forbs and shrubs were evident, and spatial heterogeneity of *F. valesiaca* and *T. sipyleus* indicated unstable vegetative patterns in heavily grazed pastures and successional changes in protected pastures. Our study results identify *F. valesiaca* and *T. sipyleus* as indicator species of vegetation suppression in condition assessments of degraded steppe rangelands.

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### 1. Introduction

One third of the 13.1 million hectares of grazing lands in Turkey is located in the Central Anatolian plateau (Anonymous, 2001). Generally, this region has been included in the Irano-Turanian phytogeographical region by Zohary and is commonly referred to as the “Central Anatolian” province (Zohary, 1973). As in most of the world, steppe vegetation in Central Anatolia has been exploited for grazing and intensive agriculture activities (Akman et al., 1984). In the region, many grazing areas have been converted to croplands, especially from the early 1950s to the late 1970s (Bakır, 1987; Büyükburç, 1983). As a consequence, remaining rangelands have been overgrazed for a long period of time, resulting in severely deteriorated vegetation. In Turkey, little is known about how grazing influences the distribution of plant species. Excessive grazing might change vegetation structure, thus upsetting ecosystem processes and biodiversity. Historically, rangeland

vegetation of Central Anatolia was changed through grazing from a tall-grass dominated state to shrub dominated, mostly *Artemisia santonicum*, rangelands (Horn, 1970; Walter, 1956). Walter (1956) asserted that in response to increased grazing pressure *Thymus sipyleus* becomes a prevailing species. Birand (1943) identified nearly 900 plant species in the region, and he pointed out that these rangelands had distinctive characteristics in common with Russia's steppe vegetation and many similar plant species. In these rangelands the two major plant species *Festuca valesiaca*, a sod forming short grass, and *T. sipyleus* ssp *rosulans*, a prostrate shrub (Bakır, 1987; Büyükburç, 1983) may be considered indicators of rangeland degradation as they are exceptionally persistent (Fırıncıoğlu et al., 2008).

Naveh and Whittaker (1979) reported that when grazing is either extensive or absent, the dominance of grasses eliminates other species and thus reduces diversity. High grazing pressure reduces diversity because only a few species are resistant to defoliation (Puerto et al., 1990). Plant diversity typically increases after the removal of herbivory (Fırıncıoğlu et al., 2007; McNaughton, 1977; Milchunas et al., 1988) and Adler and Lauenroth (2000) reported that livestock enclosures increased spatial heterogeneity. From a practical or management point of view, an important issue

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is the relationship between spatial heterogeneity and biodiversity (Adler et al., 2001). Changes in spatial heterogeneity caused by grazing imply changes in habitat diversity of consumers ranging from insects to birds and mammals (Bock et al., 1984; Dennis et al., 1998; Grant et al., 1982), as cited in Adler and Lauenroth (2000). Weber et al. (1998) concluded that grazing impacts on vegetation dynamics depended in large part on heterogeneity in grazing pressure. If grazing alters the spatial structure of an ecosystem, it will have potentially important consequences for a wide variety of ecosystem functions (Adler et al., 2001).

There is little information about how grazing affects the spatial heterogeneity of plant species. In Central Anatolian steppe grazing lands, it is presumed that overgrazing has shifted the composition of range vegetation from tall-grass to short grass and short-shrub dominant rangelands where the abundance of initial plant species (i.e., pristine state) declined with grazing over time. But how has this change in vegetation influenced spatial heterogeneity? The spatial pattern of vegetation can be influenced by two main factor groups; (1) intensity and homogeneity in grazing history, and (2) spatial and temporal variation in climate (e.g., rainfall, temperature), soil and topography (e.g., aspect, altitude and slope).

Factors such as environmental heterogeneity, ecosystem productivity, ecosystem type, and grazer selectivity may be the ultimate determinants of patterns in grazing and vegetation, but they do not control the immediate effect of grazing on spatial heterogeneity (Adler et al., 2001). The simplest definition of spatial heterogeneity is a 'departure from randomness of distribution' (Greig-Smith, 1979) or a departure from homogeneity. Since plant community composition and structure are measured with continuous variables such as percent cover, spatial heterogeneity is used in the sense of surface pattern (Adler and Lauenroth, 2000). Spatial autocorrelation analysis is a commonly used method to measure spatial heterogeneity (Adler and Lauenroth, 2000; Chang et al., 2006; Ripley, 1981). Spatial autocorrelation arises if the same variable quantified at two sites of  $d$  distance (Chang et al., 2006). Ripley (1981) and Chang et al. (2006) reported that in the autocorrelation analysis spatially explicit data collected at various locations across the landscape is used, so that their scale domains (also named as "characteristic scales") and assorting thresholds can be determined.

We hypothesize that species richness and abundance decrease with increasing abundance of *F. valesiaca* and *T. sipyleus* and that this decrease is driven by grazing. If this hypothesis is correct, these two species would respond predictably to ecosystem impacts, and could be used as indicator species. Therefore, our objective was to investigate the effects of grazing on steppe vegetation by determining whether there are patterns in the vegetation; how dominant species contribute to the patterns; and how the pattern in grazed vegetation differs from the pattern in ungrazed vegetation.

## 2. Material and methods

### 2.1. Study site

The study was conducted in 2003 in rangelands near the Field Crops Central Research Institute Experimental Station (FCCRIES), 45 km southwest of Ankara, and close to İlıkçe village range areas (Appendix 1). Prior to establishment of the Research Station in 1976, these rangelands were heavily grazed. After station establishment, its borders were fenced and these areas were protected from grazing for 27 years, while the village pastures continued to be heavily grazed by sheep and cattle. The village farmers (personal communication with Mr. Zeki Çetin) reported that before enclosure establishment, there were 1280 AU of small and large ruminants (1 AU equals 500 kg live weight) grazing 600 ha of range area

(0.47 ha/AU), which is considered very high grazing pressure. Currently 270 AU of both small and large ruminants are grazing 150 ha of native pasture (0.55 ha/AU) outside the fenced area. Over the last 30 years in the village, both rangeland area and number of livestock have been reduced dramatically, but the grazing pressure has not changed. In the region, grazing occurs year round with free access and no management practices are implemented. Limited rangeland forage in winter is augmented by allowing animals to graze stubble after cereal harvest on croplands and by feeding cereal straw, barley grain and other supplements (Firincioglu et al., 1995).

Soils are clay-loam, slightly alkaline, low in organic matter and phosphorous, high in lime, and abundant in potassium. The Central Anatolian plateau is characterized by its arid climate (300–350 mm annual rainfall), cold winters, and warm summers. Rainfall data obtained from the FCCRIES's metrological station measured a long-term average of 377 mm. Rainfall was 360 mm in 2003.

The rangelands are a typical steppe vegetation type with some dominant perennial grasses (*F. valesiaca*, *Poa bulbosa*, and *Bromus tomentellus*), annual grasses (*Bromus tectorum* and *Bromus japonicus*), and shrub species (*T. sipyleus*, *Globularia orientalis*, and *Genista albida*).

### 2.2. Methods

To investigate the effect of grazing on vegetation (i.e., spatial heterogeneity), we have compared data obtained from two grazing treatments: one long-term protected (ungrazed) and one continuously grazed. Three multi-scale vegetation plots were placed at each of the two grazing treatments (ungrazed and grazed). The plots, which were placed inside and outside the enclosures, were paired to similar soils, slopes, and aspects (Appendix 1). Ungrazed plot (U1) and grazed plot (G1) were on relatively flat terrain. The others, U2, U3, G2, and G3, were on a 20–30° NE slope. The Modified-Whittaker plot (Fig. 1) was chosen as it samples a large area (0.1 ha). Plots were placed with the long axis along the major elevation gradient (Stohlgren et al., 1999) and were sampled at the phenological maximum (peak biomass) during the third week of June. Each 20 × 50 m plot (1000 m<sup>2</sup>) had nested in it ten 0.5 × 2 m plots (quadrats), and spatial location of each quadrat was calculated as the distances from the origin (Fig. 1). The bottom left corner of the Modified-Whittaker plot (Fig. 1) was marked as the origin ( $x = 0, y = 0$ ) of the X and Y axes. The center of each 1-m<sup>2</sup> plot situated inside the nested design and their distances from the origin were calculated as the X and Y distances.

In the ten 1-m<sup>2</sup> plots, all plant species were identified and basal cover of each species, percentage of bare ground, and non-plant components (rock and stone) were estimated to the nearest percent. In addition to species data, a total of nine spatially explicit environmental variables (slope, soil depth, and some soil properties) were used in this study. The soil samples were taken from the quadrat center at 0–20 cm soil depth. At the same point, soil depths were measured with the use of an auger. Soil samples were analyzed for water saturation (%), total salt (%), lime content (%), pH, potassium (K<sub>2</sub>O; kg ha<sup>-1</sup>), phosphorus (P<sub>2</sub>O<sub>5</sub>, kg ha<sup>-1</sup>), and organic matter (%).

Plant species which could not be identified in the field were collected and identified at the herbarium of the Biology Department at Ankara Gazi University. Four specimens were not identifiable due to phenological stage, but could be classified into plant category (forbs, grasses and shrubs) and life form (annuals and perennials).

Biomass is a parameter which may best reflect the differences in community structure (Guo and Rundel, 1997). Because *F. valesiaca* was considered a pivotal species, its above ground biomass was

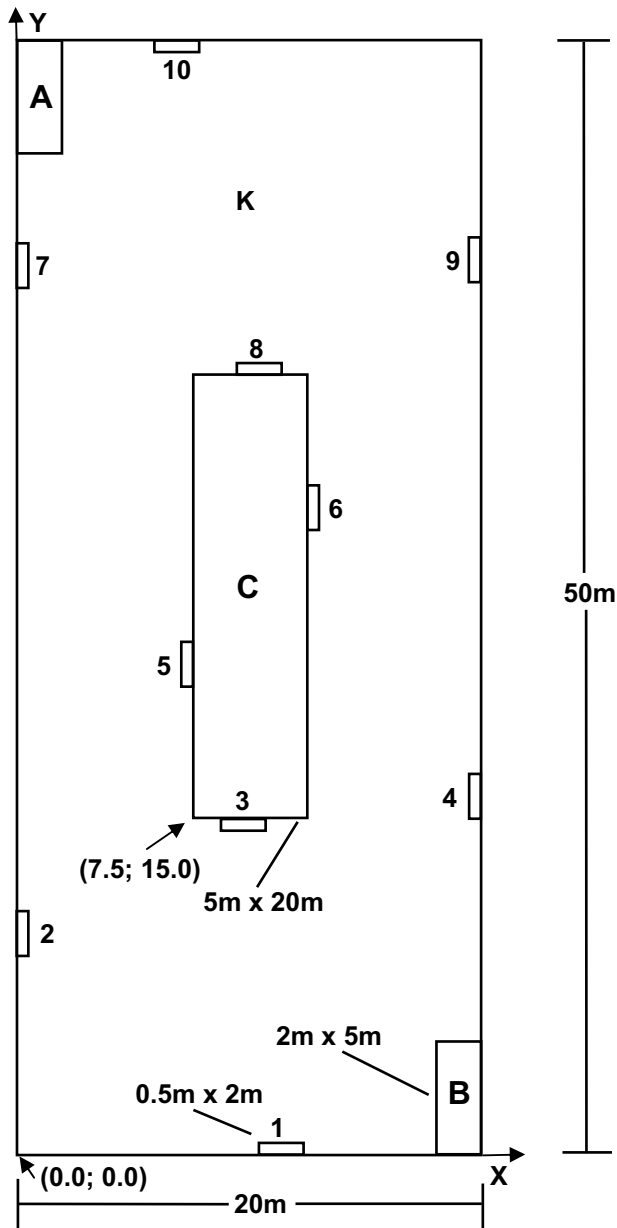


Fig. 1. The schematic presentation of Modified-Whittaker plots; coordinating and numbering of the 1-m<sup>2</sup> subplots along with the X and Y axis.

determined. After completing vegetation measurements in the 1-m<sup>2</sup> quadrats, all *F. valesiaca* plants were harvested at the ground level and biomass was determined after drying for 48 h at 70 °C in an air-forced stove.

Data analysis began with a calculation of average basal cover of the major species, and then functional groups (forbs, grasses, and shrubs). A two independent samples *t*-test was employed to determine differences between the number of species, major plant species, functional groups, and *F. valesiaca* biomass for the ungrazed and grazed treatments. Before the *t*-test, to satisfy assumptions of normality, all data after adding 1 were Log<sub>10</sub> transformed. A fitted line regression analysis was used to determine the following two relationships: species richness versus plant category (forb, grass, and shrub) covers, and *F. valesiaca* cover versus *B. tomentellus* and *T. sipyleus* covers. All *t*-test and fitted regression analyses were performed with the Minitab statistical

package, and alpha = 0.05 was used to determine significance in all tests.

To investigate relationships between vegetation and physical environmental factors, the canonical form of principle component analysis, the direct ordination method Redundancy analysis (RDA), was used. CANOCO version 4.5 (ter Braak and Milauer, 1998) was used separately for both ungrazed and grazed areas. Results of RDA were used to ordinate sites, based on the abundance and occurrence of plant species, along with environmental variables (soil and slope). When gradients are short, the relationship between vegetation response and environmental variables is likely to be linear (Ward et al., 1993). Jongman et al. (1987) recommend use of RDA for linear relationships, where the explained variance is a straight sum of square from the regression in RDA (ter Braak, 1991). A linear response model such as RDA will produce better results than a Gaussian response model such as the Detrended Correspondence Analysis when the studied gradient is short and most species are behaving monotonically over the observed range (i.e., their observed response is almost linear) (Gauch, 1982; Palmer, 1993; ter Braak and Prentice, 1988). Results of the RDA were used to ordinate species based on their abundance and occurrence in the samples along with environmental variables (soil and slope) in the 1-m<sup>2</sup> plots of the ungrazed and grazed treatments separately. Species that had an occurrence of less than 4 of a possible 30 sites were considered rare and were removed from the data matrix to avoid introducing unnecessary noise (Mentis, 1983). This removal was justified by Gauch (1982) for two reasons: (1) occurrences of rare species are usually more a matter of chance than an indication of ecological conditions, and (2) most multivariate techniques are affected very little by rare species carrying such a small percentage of the overall information of variance. Therefore, the RDA was performed with the abundance of 31 species in ungrazed and 23 species in grazed plots, and with the soil and slope environmental variables. A three-plot of the RDA demonstrates the correlation among species composition, samples (i.e., quadrats), and environmental variables (i.e., soil, slope, and soil depth) by the direction and length of lines radiating from the centroid of the ordination scores.

To detect spatial heterogeneity of the dominant species (*T. sipyleus* and *F. valesiaca*), we analyzed the autocorrelation of these individual species abundance measured as percent cover. Spatial autocorrelation analyses were employed for the ungrazed and grazed range areas using GS+ version 5.3.1. (Geo-statistics for Environmental Sciences). The calculated distances from the origin were entered as X and Y values into the data matrices and alongside the Y axis upper bounds of each 1-m<sup>2</sup> plot were defined and entered as non-uniform intervals. Isotopic correlograms were produced and Moran's *I* (Sokal and Oden, 1978) was used. Moran's *I* values range from -1 to +1, with +1 indicating perfect positive autocorrelation and -1 indicating perfect negative autocorrelation at lag distance (separation distance) class *d*. A Moran's *I* value of 0 indicates that data pairs at lag class *d* apart are not correlated to each other.

### 3. Results

#### 3.1. Vegetation composition

In the study area there were 74 plant species, of which 61 and 44 species were identified in ungrazed and grazed treatments of the 1-m<sup>2</sup> subplots, respectively (data not shown). More forb species existed in ungrazed plots (48) compared to the grazed plots (32), and the enclosure had more perennial species (48) than that of the village rangelands (33).

A comparison of several vegetation parameters of grazing effect between enclosure and village pastures revealed important

differences (Table 1). Exclosure plots had significantly ( $P < 0.01$ ) larger plant basal cover (21.8%) than village rangelands (16.2%). There were significantly ( $P < 0.01$ ) more species in ungrazed plots (13.3) than in the grazed plots (11.4). Forbs possessed significantly ( $P < 0.05$ ) larger basal cover in ungrazed plots (3.3%) than in grazed rangeland (1.6%), whereas grasses (8.1% and 5.4%) and shrubs (10.5% and 9.2%) did not differ in grazed and ungrazed plots, respectively (Table 1). Among the major plant species, *F. valesiaca* had greater ( $P < 0.05$ ) basal cover (8%) in ungrazed than in grazed plots (4.7%), whereas *T. sipyleus* acquired larger cover ( $P < 0.05$ ) in grazed plots (8.3%) than in ungrazed plots (3.6%) (Table 1). The three shrub species, *G. albida* (1.8% and 0.4%), *G. orientalis* (12.9% and 5.8%) and *Gypsophila sphaerocephala* (1.8% and 0.0%), had higher basal cover in exclosure than in village pasturelands, respectively. The basal cover of *B. tomentellus*, a perennial tall-grass, was not different between the two grazing treatments. The important forage species, *F. valesiaca* had nearly 100% more plant biomass in the ungrazed plots ( $110.6 \text{ g } 1\text{-m}^{-2}$ ) than in the grazed plots ( $61.9 \text{ g } 1\text{-m}^{-2}$ ) (Table 1).

### 3.2. Vegetation-spatial pattern and species richness

An examination of relationships between dependent variables is important in the context of determining grazing impact, because the effects of the major species on species composition can be used to infer species suppression and diversity. Vegetation patterns were explained by changes in plant composition. Regression analyses (quadratic and linear) for species richness versus plant category cover, *F. valesiaca* cover versus forb, *B. tomentellus*, *T. sipyleus* covers, and *T. sipyleus* cover versus grass cover are illustrated in Fig. 2. Significant quadratic relationships were found between forb cover and species richness in both ungrazed ( $R^2 = 20.5\%$ ,  $P < 0.05$ ) and grazed treatments ( $R^2 = 22.6$ ,  $P < 0.05$ ) (Fig. 2a), while grass cover was statistically unrelated to number of species (Fig. 2b). Shrub cover in the exclosure was negatively associated with species richness ( $R^2 = 43.6\%$ ,  $P < 0.001$ ), whereas it had a quadratic

relationship in villages' pastures ( $R^2 = 28.5\%$ ,  $P < 0.01$ ) (Fig. 2c). *T. sipyleus* cover had a quadratic relationship with species richness in grazed plots ( $R^2 = 27.2\%$ ,  $P < 0.05$ ) (Fig. 2d). There was a quadratic relationship between *F. valesiaca* cover and forb cover in ungrazed plots ( $R^2 = 34.7\%$ ,  $P < 0.01$ ) (Fig. 2e), and *T. sipyleus* cover was similarly related to grass cover ( $R^2 = 45.0\%$ ,  $P < 0.01$ ) (Fig. 2f). There was a negative correlation between *F. valesiaca* cover and *B. tomentellus* cover in grazed plots ( $R^2 = 23.8\%$ ,  $P < 0.01$ ) (Fig. 2g), and between *F. valesiaca* cover and *T. sipyleus* cover in ungrazed plots ( $R^2 = 22.4\%$ ,  $P < 0.01$ ) (Fig. 2h).

The isotopic correlograms for spatial patterns with Moran's *I*, based on plant basal cover of *F. valesiaca* and *T. sipyleus* in ungrazed and grazed plots, are illustrated in Fig. 3. *F. valesiaca* cover in all plots, except G1, were spatially autocorrelated at different scales, changing from negative to positive (Fig. 3a). In U3, this alteration occurred sharply at short distances. In G1 (flat area), the autocorrelation of *F. valesiaca* cover was near zero (Fig. 3a). *T. sipyleus* cover had relatively high autocorrelations in plots U2 and G3, and was relatively low in U1 and almost all negative in G1 (Fig. 3b). *T. sipyleus* cover had quite high autocorrelations, changing at short distance in plots U2 and G3 (Fig. 3b). In flat range areas, autocorrelation tended to be low, and was especially apparent for *F. valesiaca* cover in G1, and for *T. sipyleus* cover in U1.

### 3.3. Vegetation–environment relationship

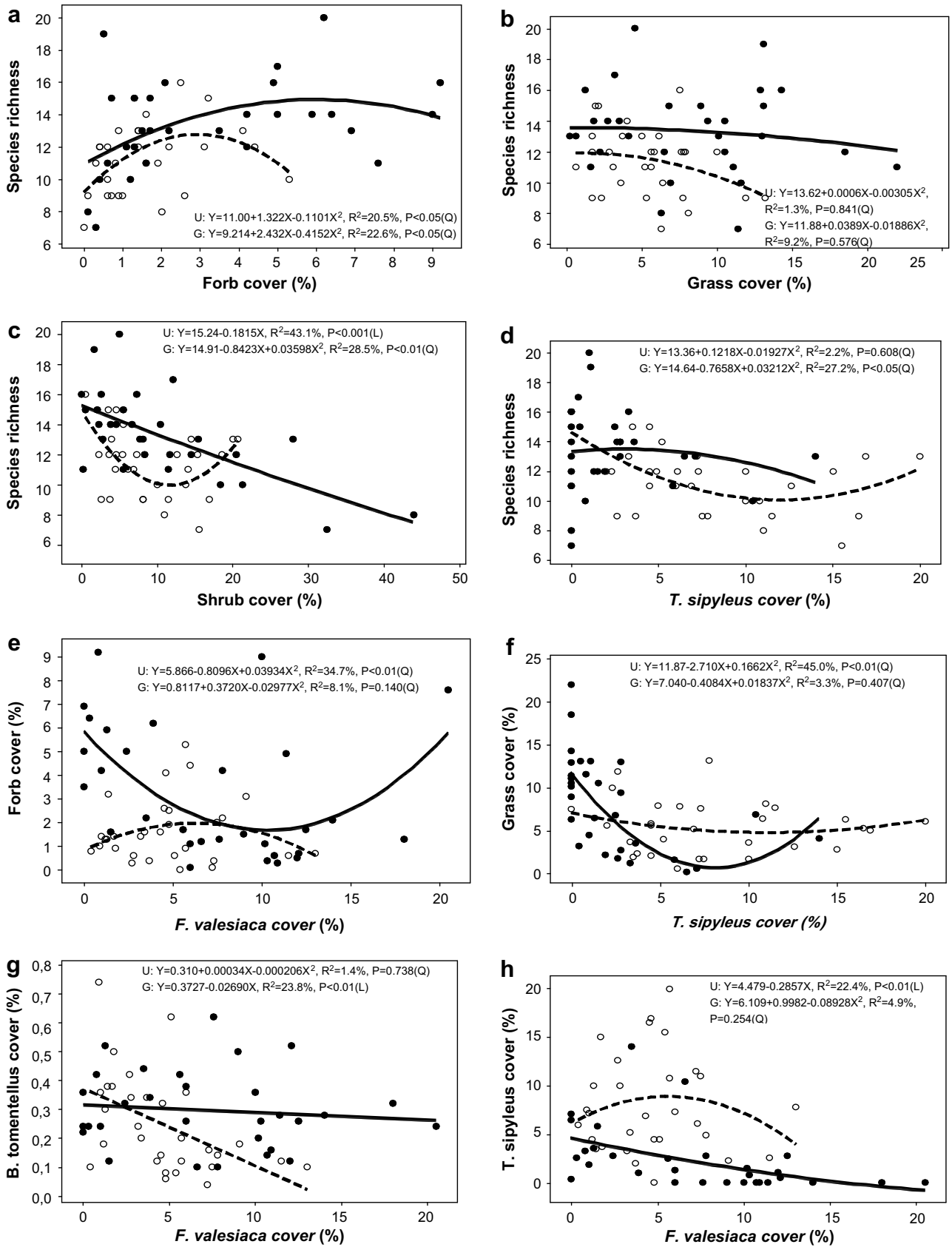
Results of the RDA are presented in Appendix 2 and Fig. 4 (tri-plot). In ungrazed and grazed plots cumulative variances of the first and second axis of the RDA explain 53.7% and 45.9% of total variance, respectively. In both treatments the first canonical axis was significant ( $P < 0.001$ ). The RDA subdivided species and samples (quadrats) into cluster groups (Fig. 4).

In the exclosure (Fig. 4a), samples taken in the flat plot (U1–quadrats from 1 to 10) were placed on the right upper quarter of the tri-plot, while quadrats sampled in sloping range areas (U2 and U3–quadrats from 11 to 30) were mostly positioned on the left half of

**Table 1**  
Percent basal cover actual and normalized with  $\text{Log}_{10}(X+1)$  transformation of total plant, and some major plant species, and other vegetation attributes, species richness, *Festuca valesiaca* biomass and steam in ungrazed (U) and grazed (G) plots.

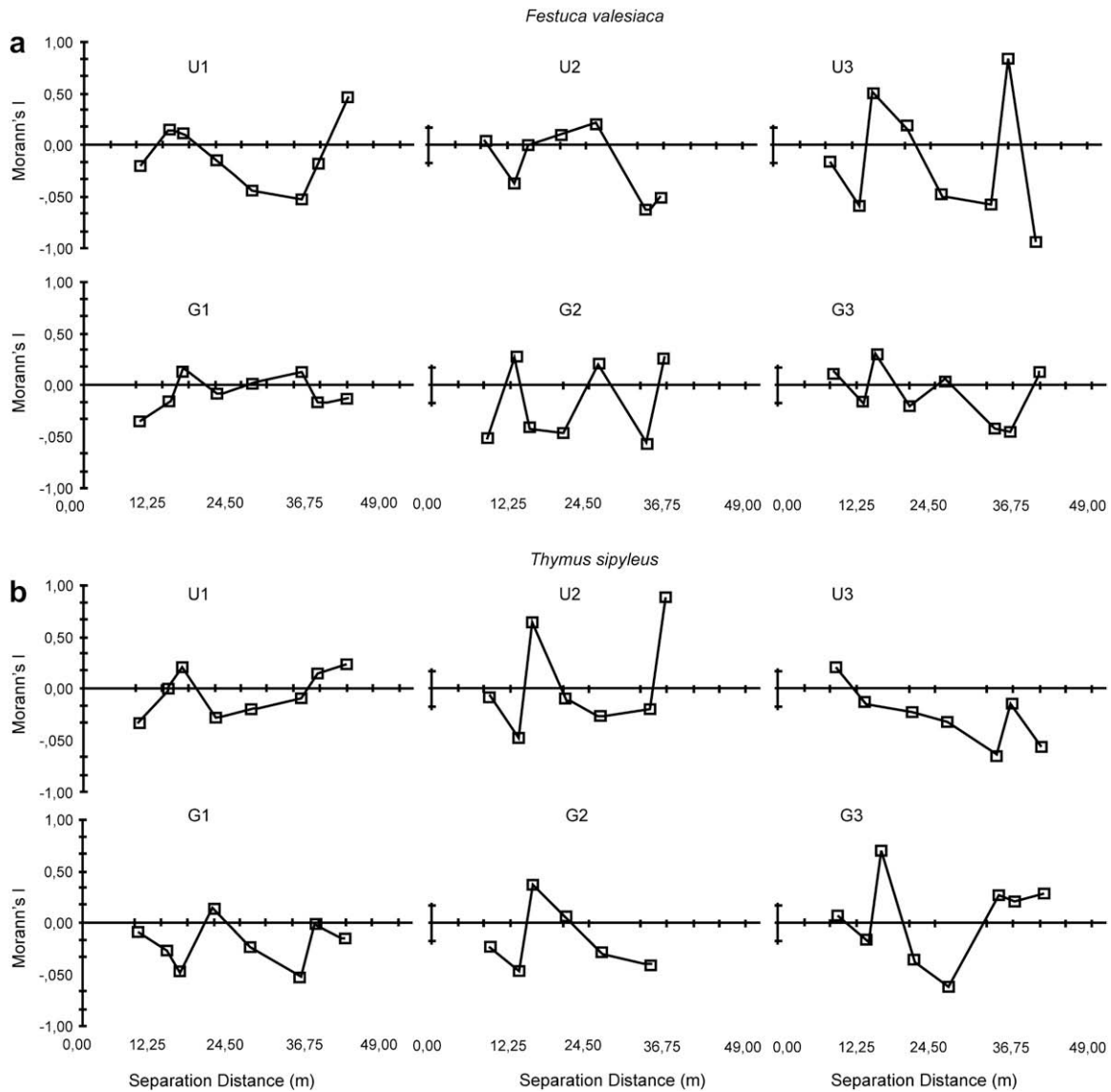
Plant categories and species	Treatment	n	Actual cover (%)	Normalized cover ( $X \pm \text{SEM}$ )	P-value
Total plant	U	30	21.82	$1.328 \pm 0.029$	<b>0.005</b>
	G	30	16.23	$1.205 \pm 0.031$	
Forbs	U	30	3.25	$0.537 \pm 0.053$	<b>0.013</b>
	G	30	1.63	$0.371 \pm 0.037$	
Grasses	U	30	8.08	$0.856 \pm 0.061$	0.163
	G	30	5.41	$0.753 \pm 0.042$	
Shrub	U	29	10.49	$0.890 \pm 0.076$	0.669
	G	30	9.19	$0.930 \pm 0.051$	
<i>Festuca valesiaca</i>	U	27	8.00	$0.856 \pm 0.064$	<b>0.036</b>
	G	30	4.66	$0.685 \pm 0.047$	
<i>Bromus tomentellus</i>	U	30	0.30	$0.11 \pm 0.01$	0.150
	G	30	0.25	$0.09 \pm 0.01$	
<i>Thymus sipyleus ssp rosulans</i>	U	20	3.62	$0.57 \pm 0.06$	<b>0.010</b>
	G	29	8.26	$0.91 \pm 0.04$	
<i>Genista albida</i>	U	16	1.77	$0.38 \pm 0.06$	<b>0.001</b>
	G	5	0.43	$0.15 \pm 0.02$	
<i>Globularia orientalis</i>	U	19	12.89	$0.98 \pm 0.10$	0.126
	G	7	5.76	$0.78 \pm 0.09$	
<i>Gypsophila sphaerocephala</i>	U	12	1.77	$0.34 \pm 0.08$	–
	G	0	0.00	$0.00 \pm 0.00$	
Other vegetation attributes	Treatment	n	Actual value	Normalized value ( $X \pm \text{SEM}$ )	P-value
Species richness (number of species in $1\text{-m}^{-2}$ )	U	30	13.3	$1.148 \pm 0.017$	<b>0.006</b>
	G	30	11.4	$1.086 \pm 0.014$	
<i>Festuca</i> biomass ( $\text{g } 1\text{-m}^{-2}$ )	U	27	110.6	$1.852 \pm 0.098$	–
	G	30	61.9	$1.671 \pm 0.063$	

n = Number of plots with plant species; SEM = standard error of the mean; bold P-value = significant differences; – = data not normalizable.



**Fig. 2.** Regression-fitted lines (quadratic (Q) and linear (L)); the species richness versus (a) forb, (b) grass, (c) shrub, and (d) *T. sipyleus*, and the basal covers of (e) *F. valesiaca* versus forb, and (f) *T. sipyleus* versus grass, and *F. valesiaca* versus (g) *B. tomentellus* and (h) *T. sipyleus* in ungrazed and grazed pastures. Ungrazed data are solid lines and closed circles and grazed data are dashed lines and open circles.





**Fig. 3.** Isotopic correlograms; illustrating the spatial patterns with Moran's  $I$ , based on plant basal cover of a. *Thymus sipyleus* and b. *Festuca valesiaca*, (1) ungrazed (U1, U2, U3) and (2) grazed (G1, G2, G3) plots.

axis 1. According to sample (quadrats) species positions, three groups appeared. Group I contained *Helianthemum ledifolium*, *P. bulbosa*, *Alyssum pateri ssp pateri*, and *Scabiosa rotata*, which are species that regularly occur in the flat ungrazed range area. Group II consisted of *T. sipyleus*, *Onobrychis armena*, *Hedysarum cappadocicum*, *Helianthemum canum*, *Jurinea pontica*, *Euphorbia macroclada*, *Galium incanum*, *Hedysarum varium*, and *G. sphaerocephala*, which are species mostly associated with sloping rangelands of the enclosures. Group III contained *Stipa lessingiana*, *Vinca herbacea*, *Teucrium polium*, and *Paracaryum racemosum var. racemosum*, which only occurred in sloping plots of grazing enclosures. Species placed outside of these groups occurred in both sloping and flat areas. In ungrazed plots, *F. valesiaca* was the most abundant species in flat areas, whereas *T. sipyleus* was the most abundant species in sloping sites.

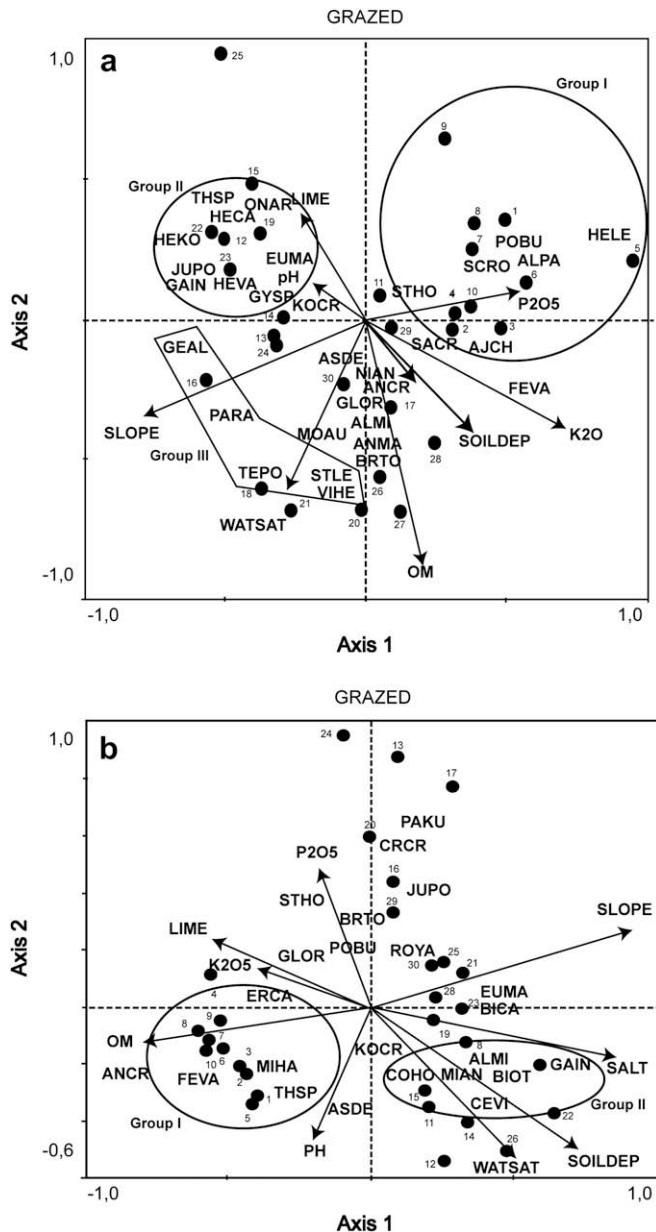
In grazed plots (G1, G2 and G3), the quadrats were placed mainly according to species and samples (Fig. 4b). Plots in flat rangeland (G1-quadrats from 1 to 10) appeared on the left bottom quarter of the tri-plot, and samples taken in sloping rangelands (G2, G3-quadrats from 11 to 30) were placed on the right half of the tri-plot. Two groups appeared in the tri-plot. Group I consisted of *F. valesiaca*,

*Minuartia hamata*, and *T. sipyleus*, located in flat pasturelands. Group II consisted of *Alyssum minus var minus*, *Convolvulus holosericeus*, *Minuartia anatolica*, unidentifiable-forb, *G. incanum*, and *Centaurea virgata*, mostly located in sloping rangelands.

In ungrazed areas, the flat plots had higher potassium and phosphorous content, while sloping plots had greater lime and pH content and water saturation (Fig. 4a). In grazed areas, flat plots had greater potassium, phosphorous, lime, and organic matter content in soil samples, whereas sloping pastures possessed more soil salt and water saturation values and had deeper soils (Fig. 4b).

#### 4. Discussion and conclusions

This study was an attempt to address the issue of heavy grazing effects on spatial patterns of plant communities in steppe pastures. Degradation of rangelands is becoming an increasing concern in the Central Anatolian steppe. To investigate the effect of grazing on spatial patterns, our study included data from grazed and ungrazed rangeland areas. An assumption of our study was that before an enclosure was built, the vegetation and soils were similar (Stohlgren et al., 1999).



**Fig. 4.** Triple plots of species, samples (quadrats) and environmental variables of Redundancy Analysis (RDA) in (a) ungrazed and (b) grazed plots. Abbreviations: A) Species: AJCH (*Ajuga chamaepitys*), ALPA (*Alyssum pateri* ssp. *pateri*), ALMI (*Alyssum minus* var. *minus*), ANCR (*Anthemis cretica* ssp. *anatolica*), ANMA (*Androsace maxima*), ASDE (*Astragalus densifolius* ssp. *densifolius*), BICA (Unidentifiable-forb), BIOT (Unidentifiable-forb), BRTO (*Bromus tomentellus*), CEVI (*Centaurea virgata*), CRCR (*Crupina crupinastrum*), COHO (*Convolvulus holosericeus*), EUMA (*Euphorbia macroclada*), FEVA (*Festuca valesiaca*), KOCR (*Koeleria cristata*), MIAN (*Minuartia anatolica*), MIHA (*Minuartia hamata*), HELE (*Helianthemum ledifolium*), HECA (*Hedysarum cappadocicum*), HEKO (*Helianthemum canum*), HEVA (*Hedysarum varium*), GLOR (*Globularia orientalis*), GYSP (*Gypsophila sphaerocephala*), GAIN (*Galium incanum*), GEAL (*Genista albida*), MIAN (*Minuartia anatolica*), MOAU (*Moltkia aurea*), PAKU (*Paronychia kurdica*), PARA (*Paracaryum racemosum* var. *racemosum*), POBU (*Poa bulbosa*), ROYA (Unidentifiable-forb), STLE (*Stipa lessingiana*), SCRO (*Scabiosa rotata*), SACR (*Salvia cryptantha*), STHO (*Stipa holosericea*), ONAR (*Onobrychis armena*), JUPO (*Jurinea pontica*), THSP (*Thymus sipyleus* ssp. *rosulans*), TEPO (*Teucrium polium*), VIHE (*Vinca herbacea*). B) Environmental variables: Soil depth-cm (SOILDEP), Water saturation - % (WATSAT), Total salt - % (SALT), pH, Lime content - % (LIME), Potassium content -  $\text{kg ha}^{-1}$  ( $\text{K}_2\text{O}$ ), Phosphorous content -  $\text{kg ha}^{-1}$  ( $\text{P}_2\text{O}_5$ ), Organic Matter - % (OM), Slope-degree (SLOPE).

In this study substantial differences in species richness were measured between ungrazed and grazed areas. Grazing has been reported to decrease species richness in nutrient-poor terrestrial systems and increase it in nutrient-rich systems (Proulx and

Mazumder, 1998). In the nutrient-poor soil in this study, protection increased species richness; 14.3% more species were recorded in the enclosure compared to continuously grazed pastureland, indicating that heavy grazing reduced species richness. In comparison with the enclosure, year-round grazing altered plant composition through decreasing total plant (25.6% less), forb (50.2% less), grass (33.1% less), and *F. valesiaca* cover (41.8% less) while it substantially increased *T. sipyleus* cover (56.2% more). The variation in the abundance of major species between ungrazed and grazed plots was particularly pronounced for *F. valesiaca* and *T. sipyleus* which are common species in deteriorated range areas with shallow soil and low fertility (Firincioglu et al., 2008).

The reaction of a plant species to grazing depends upon the ability to compensate for lost biomass and the relative impact of removal on competitive relationships in the canopy (Milchunas and Lauenroth, 1993). Variations in plant species abundance reflect vegetation patterns, whereas change in major species cover is a key factor in shaping the responses of the plant community to grazing. The response of a plant community to grazing is an indication of vegetation resistance to disturbance. Milchunas et al. (1988) suggested that arid conditions promote the development of grazing resistance traits. Our analysis of vegetation community composition suggested greater impacts of grazing on forbs than on grasses. However, forbs were favored in grazed situations when they were prostrate, fast spreading rosette plants (e.g., *C. holosericeus* and *O. armena*) or upright with defense mechanisms such as chemical compounds (e.g., *E. macroclada*). The major shrub species (*G. orientalis*, *G. albida*, and *G. sphaerocephala*) were also reduced in grazing areas. *T. sipyleus* provides an incremental structural complexity to grazing lands. As a dominant dwarf shrub it is less likely to decrease under grazed versus ungrazed conditions, and in this study it had twice as much cover in grazed compared to ungrazed areas. In this context, *T. sipyleus* can be regarded as an indicator species of disturbance for its extreme persistence in intensively grazed areas.

Alteration in grassland structure and diversity, due to grazing, are primarily functions of productivity and evolutionary grazing history (Milchunas and Lauenroth, 1993), possibly determining species composition and prevailing functional groups that characterize the plant communities of these steppe rangelands. In this study grasses, especially tiller forming grasses (e.g., *F. valesiaca*, *P. bulbosa*, and *B. tomentellus*), in contrast to forbs, were encouraged by grazing because of their compensatory re-growth from basal meristems even on nutrient-poor soils they are able to tolerate to repeated biomass loss and trampling (Crawley, 1992; McNaughton, 1982; Peintinger, 1999).

Noy-Meir et al. (1989) observed tall perennial and tall annual grasses dominating ungrazed sites, whereas small, prostrate annuals were abundant in heavily grazed sites, as cited in Milchunas and Lauenroth (1993). When a disturbance occurs regularly and over a long period, plant populations can evolve a strategy enabling them to survive the disturbance, and there are many examples of adaptations to permanent or periodically unfavorable conditions (Margalef, 1974), as cited in Fernandez et al. (1993). In this study, short plant canopies and generally prostrate growth could be interpreted as adaptations to grazing disturbance. These adaptive devices are illustrative of *F. valesiaca* and *T. sipyleus*. *F. valesiaca* is a perennial dominant short grass in heavily grazed barren rangelands, that forms a sod, has erect stems 10–60 cm tall, and is cold and drought tolerant (Gençkan, 1983). *F. valesiaca*, an increaser, is somewhat preferred by grazing animals (Anonymous, 2005). *T. sipyleus* Boiss. occurs as a semi-shrub invader in the weedy species dominated pastures. During winter sheep graze its shoots (Bakır, 1987), and it has a prostrate stature with strongly scented white or pink flowers and 3–6 mm long leaves (Anonymous, 2005).

Changes in dominant species due to grazing can be related to similar independent variables such as changes in species composition (Milchunas and Lauenroth, 1993). The significant relationship of *F. valesiaca* cover with *T. sipyleus* and *B. tomentellus* covers indicate the importance of spatial patterns in determining vegetation assemblages (Fig. 2g, h).

Forbs, with the greatest number of species, had a quadratic relationship with species richness in both treatments. Species richness decreased when forb cover was at its lowest and highest amounts (Fig. 2a). This quadratic variation in species richness has been attributed to the coexistence of contrasting growth forms (Wilson and Tilman, 2002) along successional (Denslow, 1980), wetland (Shipley et al., 1991), and mountain side gradients (Wilson, 1994). There were proportionally less (44%) forb species in grazed areas, where forbs potentially respond more negatively to grazing than graminoids because they have a reduced ability to regenerate (Wilmans, 1998).

An increase in the shrub cover in the ungrazed areas was associated with decreased plant species richness indicating that shrubs were suppressing plant diversity. In grazed areas species richness was greatest when shrub cover was at both lowest and highest abundance (Fig. 2c) which is opposite the response measured with forb cover.

In grazed plots, *T. sipyleus* cover had a quadratic pattern similar to shrub cover (Fig. 2d), with its lowest and highest cover resulting in increased species richness. In ungrazed plots, increased and decreased cover of *T. sipyleus* was associated with increases in grass cover. At a cover of 8% *T. sipyleus*, grass cover was at a minimum of near 1% basal cover (Fig. 2f).

In the enclosure, moderate covers of *F. valesiaca* were associated with the minimum values of forb cover (Fig. 2e), with increases or decreases in *F. valesiaca* cover resulting in increases in forb cover. In the grazed areas, as *F. valesiaca* cover increased *B. tomentellus* basal cover declined and, in the ungrazed areas, as *F. valesiaca* cover increased *T. sipyleus* cover decreased (Fig. 2g, h). The two negative associations (e.g., *F. valesiaca* versus other species) suggest competitiveness for resources, whereas a positive association would suggest that the two species coexist and share the same resources. Adler and Lauenroth (2000) reported that spatial patterns generated by individual plant interactions are apparent only in ungrazed sites. These interactions are somewhat evident in our study where there are significant relationships among the dominant species in addition to dominant species and species richness that were mostly determined in the ungrazed plots. This relationship might be because of spatial processes, which are not disturbed in the absence of grazing, but could be overwhelmed due to the selection pressure and mortality caused by grazing. Biomass may better reflect differences in community structure (Guo and Rundel, 1997). *F. valesiaca* produced 44.3% more biomass in ungrazed plots, where it was negatively associated with decreased *T. sipyleus* cover (Fig. 2h).

Given the geographical homogeneity of the study area, it is probable that soil properties related to slope are controlling vegetation pattern. As Wei and Christina (1995) explained it, spatial assemblages of the vegetation appear to be the rule rather than exception in many vegetation types and plant communities. Moran's *I* results in the isotopic correlograms showed that dominant components of vegetation tend to be non-randomly distributed in sloping range areas of both treatments and to be aggregated spatially (Fig. 3). *F. valesiaca*, in the flat plots of grazed treatments, and *T. sipyleus*, in the flat plots of ungrazed treatments, were spatially homogenous in distribution. Based on the definition of spatial heterogeneity, higher spatial dependence in sloping pastures represents an increase in spatial heterogeneity relative to topography and grazing. Therefore, spatial differentiation of plant

communities, which are based on species occurrences in an array of sample plots, depends on the spatial variation of environmental properties (Ehrenfeld et al., 1997). While *T. sipyleus* is extremely dominant in grazed treatments, patches of *F. valesiaca* dominated in sites where *T. sipyleus* cover decreased in ungrazed range areas. Our results revealed that a key difference in patterns between treatments is the occurrence of *F. valesiaca* patches and reduced *T. sipyleus* cover in ungrazed compared to grazed plots. We determined that there was considerable spatial variability in vegetation. This variability may be typical for these steppe rangelands largely as a result of topography and soil. These factors appear to have an impact on the dominance of plant communities where *F. valesiaca* and *T. sipyleus* are the prevailing species.

Environmental gradients are commonly and often implicitly assumed to control the distribution of plant species and plant associations (Kent and Coker, 1992), as cited in Ehrenfeld et al. (1997). In both treatments, RDA successfully subdivided the species and samples into groups according to their abundance and occurrences in the samples (Fig. 4). The investigation of vegetation gradients enables an initial understanding of plant variation in relation to environmental gradients. The degree to which variation in environmental properties affects the structure of vegetation may thus reflect the consistency of spatial patterns. In protected pastures *F. valesiaca* and *T. sipyleus* were situated on the opposite sides of the axis 1 (flat or sloping rangelands, respectively) (Fig. 4a). In grazed plots, the vegetation gradient was inversely established to that of the ungrazed, and *F. valesiaca* and *T. sipyleus* were closely located to each other in the same quarter (in flat plots) of the tri-plot (Fig. 4b).

Vegetation patterns were explained by the increasing abundance of *F. valesiaca* cover in ungrazed plots and *T. sipyleus* cover in grazed plots. *F. valesiaca* was correlated with forbs and *T. sipyleus* covers in the enclosures, while it was negatively correlated with *B. tomentellus* cover in grazed plots. These relationships appear to be casual. In fact, *F. valesiaca* dominated the successional trajectory in the protected areas, which is consistent with *F. valesiaca* acting as an invasive transformer species. For future changes following continued exclusion of grazing, we hypothesize that *F. valesiaca* cover will probably continue to increase in the study area and ultimately influence ecosystem function. Because species richness may have a negative trend with age of enclosures in some ecosystems (Bokdam and Gleichman, 2000; Olf and Ritchie, 1998), we conclude that long-term exclusion of grazing may not necessarily increase species richness.

Based on this study four broad conclusions can be made: (1) *F. valesiaca* and *T. sipyleus* had a significant effect in shaping the vegetation pattern, (2) reduction in species richness with increasing covers of shrubs was evident in ungrazed pastures, indicating an influence on plant succession, (3) the spatial heterogeneity of both *F. valesiaca* and *T. sipyleus* was obvious for both treatments, demonstrating an unstable vegetative pattern in grazed treatments and successional changes in protected treatments, and (4) both *F. valesiaca* and *T. sipyleus* are useful as suppressive indicator species for rangeland assessments.

## 5. Practical implications

Heavy grazing negatively affects the quality of steppe vegetation, from both a conservation and production point of view. The plant communities of the Central Anatolian steppe rangelands are typically species poor, with the dominance of a few short grasses and dwarf shrubs. This rangeland vegetation is of considerable importance both agriculturally and ecologically, as in other arid land grazing systems throughout the world. The keys to maintaining sustainability are to preserve a substantial cover of



palatable species, and to prevent the dominance of species that are unproductive or that alter community structure. Understanding the ecology of the species present in the rangeland is critical to predicting the effects of management. In arid systems like the Central Anatolian steppes, at high grazing intensities, dwarf shrubs and short grasses increase at the expense of tall perennial grasses and forbs. In long-disturbed range vegetation, dominated with *F. valesiaca* and *T. sipyleus*, it is expected that proper grazing management can reverse the ever worsening degradation situation, following natural successional processes that will ultimately result in an improved rangeland vegetation condition.

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### Appendix. Supplementary material

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.jaridenv.2009.05.012.

### References

- Adler, P.B., Lauenroth, W.K., 2000. Livestock exclusion increases the spatial heterogeneity of vegetation in Colorado shortgrass steppe. *Applied Vegetation Science* 3, 213–222.
- Adler, P.B., Raff, D.A., Lauenroth, W.K., 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128, 465–479.
- Akman, Y., Ketenöglü, O., Quézed, P., Demirörs, M., 1984. Asyntaxonomic study of steppe vegetation in Central Anatolia. *Phytocoenologia* 12, 563–584.
- Anonymous, 2001. The General Agriculture Census. State Statistic Institution, Ankara.
- Anonymous, 2005. Pasture Plants Guidebook. Ministry of Agriculture and Rural Affairs, Ankara, Turkey, pp. 136, 187.
- Bakır, Ö., 1987. Range Management. Ankara University, Ankara, Turkey. Agriculture Faculty Publication: 992, Textbook: 292, 5–10.
- Birand, A.A.H., 1943. Our Steppe as the Rangeland and its Matters in Terms of Botany. Agriculture High School, Ankara, Turkey. Publication No: 1.
- Bock, C.E., Bock, J.H., Kenney, W.R., Hawthorne, V.M., 1984. Responses of birds, rodents, and vegetation to livestock enclosure in semidesert grassland site. *Journal of Range Management* 37, 239–242.
- Bokdam, J., Gleichman, J.M., 2000. Effects of grazing by free-ranging cattle on vegetation dynamics in a continental north-west European heathland. *Journal of Applied Ecology* 37, 415–431.
- Büyükbırcı, U., 1983. The Properties and Restoration Possibilities of the Central Anatolian Rangelands. Grassland and Animal Husbandry Research Institute, Ankara, Turkey. Publication No: 80.
- Chang, C.R., Leen, P.F., Bai, M.L., Lin, T.T., 2006. Identifying the scale thresholds for field-data extrapolation via spatial analysis of landscape gradients. *Ecosystems* 9, 200–214.
- Crawley, M.J., 1992. Plant-herbivore dynamics. In: Crawley, M.J. (Ed.), *Plant Ecology*. Blackwell, Oxford, UK, pp. 401–474.
- Dennis, P., Young, M.R., Gordon, I.J., 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecological Entomology* 3, 253–264.
- Denslow, J.S., 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46, 18–21.
- Ehrenfeld, J.G., Han, X., Parsons, W.F.J., Zhu, W., 1997. On the nature of environmental gradients: temporal and spatial variability of soils and vegetation in the New Jersey pinelands. *Journal of Ecology* 85, 785–798.
- Feranandez, A.R., Laffarga, J.M., Ortega, F., 1993. Strategies in Mediterranean grassland annuals in relation to stress and disturbance. *Journal of Vegetation Science* 4, 313–322.
- Fıncıoğlu, H.K., Christiansen, S., Lamont, E.J., Unal, S., Peskircioglu, M., Beniwal, S.P.S., 1995. Village, farm, and pasture resource assessment in planning a forage, livestock, and range improvement project for the central highlands of Turkey. In: Haddad, N., Tutwiller, R., Thomson, E. (Eds.), *The Proceedings of the Regional Symposium on Integrated Crop-livestock Systems in the Dry Areas of West Asia and North Africa*, Amman, Jordan, pp. 39–50.
- Fıncıoğlu, H.K., Seefeldt, S.S., Şahin, B., 2007. The effects of long-term grazing enclosures on range plants in the Central Anatolian region of Turkey. *Environmental Management* 39, 326–337.
- Fıncıoğlu, H.K., Şahin, B., Seefeldt, S.S., Mert, F., Hakyemez, B.H., Vural, M., 2008. Pilot study for an assessment of vegetation structure for steppe rangelands of Central Anatolia. *Turkish Journal of Agriculture and Forestry* 32, 401–414.
- Gauch, H.G., 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge, USA, 298 pp.
- Gençkan, S., 1983. *Forage Crops Cultivation*. Textbook. Aegean University, İzmir, Turkey, Agriculture Faculty, Publication number: 467, Bornova, pp. 318–320.
- Grant, W.E., Birney, E.C., French, N.R., Swift, D.M., 1982. Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetation cover. *Journal of Mammalogy* 63, 248–260.
- Greig-Smith, P., 1979. Pattern in vegetation. *Journal of Ecology* 67, 755–779.
- Guo, Q., Rundel, P.W., 1997. Measuring dominance and diversity in ecological communities: choosing the right variable. *Journal of Vegetation Science* 8, 405–408.
- Horn, V., 1970. *Rangeland Problems in Terms of the Livestock Feeding*. Aegean University, İzmir, Turkey, Agriculture Faculty, Publication No: 163.
- Kent, M., Coker, P., 1992. *Vegetation Description and Analysis. A Practical Approach*. CRC Press, Boca Raton, FL, USA.
- Jongman, R.H.G., ter Braak, C.J.F., van Tongeren, O.F.R., 1987. *Data Analysis in Community and Landscape Ecology*. Pudoc, Wageningen, Holland.
- Margalef, R., 1974. *Ecologia*. Omega, Barcelona, Spain, 951 pp.
- McNaughton, S.J., 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *American Naturalist* 111, 515–525.
- McNaughton, S.J., 1982. Compensatory plant growth as a response to herbivory. *Oikos* 40, 329–336.
- Mentis, M.T., 1983. Towards objective veld condition assessment. *Proceedings of the Grassland Society of Southern Africa* 18, 77–80.
- Milchunas, D.G., Sala, O.E., Lauenroth, W., 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* 132, 87–106.
- Milchunas, D.G., Lauenroth, W.K., 1993. Quantitative effects of grazing on vegetation and soil over a global range of environments. *Ecological Monographs* 63, 327–366.
- Naveh, Z., Whittaker, R.H., 1979. Structural and floristic diversity of shrublands and woodlands in northern Israel and other Mediterranean areas. *Vegetation* 41, 171–190.
- Noy-Meir, I., Gutman, M., Kaplan, Y., 1989. Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology* 77, 290–310.
- Olf, H., Ritchie, M.E., 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution* 13, 261–265.
- Palmer, M.W., 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* 74, 2215–2230.
- Peintinger, M., 1999. The effects of habitat area, management and altitude on species diversity in montane wetlands. Ph.D. thesis, University of Zürich, Germany.
- Proulx, M., Mazumder, A., 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* 79 (8), 2581–2592.
- Puerto, A., Rico, M., Matias, M.D., Garcia, J.A., 1990. Variation in structure and diversity in Mediterranean grasslands related to trophic status and grazing intensity. *Journal of Vegetation Science* 1, 445–452.
- Ripley, B.D., 1981. *Spatial Statistics*. Wiley, New York, New York, USA.
- Sokal, R.R., Oden, N.L., 1978. Spatial autocorrelation in biology 1. Methodology. *Biological Journal of the Linnean Society* 10, 199–228.
- Shipley, B.P., Keddy, A., Gaudet, C., Moore, D.R.J., 1991. A model of species density in shoreline vegetation. *Ecology* 72, 1658–1667.
- Stohlgren, T.J., Schell, L.D., Heuvel, B.V., 1999. How grazing and soil quality affect native and exotic plant diversity in rocky mountain grasslands. *Ecological Applications* 9, 46–64.
- ter Braak, C.J.F., Prentice, I.C., 1988. A theory of gradient analysis. *Advances in Ecological Research* 18, 271–317.
- ter Braak, C.J.F., Milauer, S., 1998. CANOCO version 4.5.
- ter Braak, C.J.F., 1991. CNOCO – AFORTRAN Program for Canonical Community Ordination by (Partial) (Detrended) (Canonical) Correspondence Analysis, Principle Component Analysis And Redundancy Analysis (version 2.2). Technical Report LWA-88-02. Agricultural Mathematics Group, Wageningen, Holland.
- Walter, H., 1956. The problems of the Central Anatolia Steppe. *Die Naturwissenschaften* 5, 97–102.
- Ward, D., Olsvig-Whittaker, L., Lawes, M., 1993. Vegetation–environment relationship in Negev desert erosion cirque. *Journal of Vegetation Science* 4, 83–94.
- Weber, G.E., Jeltsch, F., Van Rooyen, N., Milton, S.J., 1998. Simulated long-term vegetation response to grazing heterogeneity in semi-arid rangelands. *Journal of Applied Ecology* 35, 687–699.
- Wei, Z., Christina, S., 1995. Small-scale species dynamics in semi-arid steppe vegetation in Inner Mongolia. *Journal of Vegetation Science* 6, 583–592.
- Wilms, O., 1998. *Ökologische Pflanzensoziologie*. Quelle and Meyer, Heidelberg, Germany.
- Wilson, S.D., 1994. Biomass allocation near an alpine tree line: cause and consequences for diversity. *Ecoscience* 1, 185–189.
- Wilson, S.D., Tilman, D., 2002. Quadratic variation in old-field species richness along gradients of disturbance and nitrogen. *Ecology* 83 (2), 492–504.
- Zohary, M., 1973. *Geobotanical Foundations in the Middle East*, vol. 1–2. G Fischer Verlag, Stuttgart, Germany.