

The effects of aridity and grazing on the relation between the dominant shrub *Artemisia kopetdaghensis* and plants under its canopy

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Abstract

Aridity and intensive grazing have been confirmed to affect the facilitative effects of dryland shrubs. However, their combined effects on plant-plant interactions have rarely been tested. To test how these two factors affect relations between plants, we analyzed 144 plots (under shrub canopy vs. open areas) at 12 sampling areas established in the conditions of two grazing regimes (high grazing vs. low grazing intensity) and two different climatic regions (arid vs. semi-arid) in northeastern Iran. A dominant shrub, *Artemisia kopetdaghensis*, was selected as the model species. Further, we studied changes in plant life strategies along the combined grazing and aridity stress gradients. We used relative interaction indices to test the outcomes of plant-plant interactions, calculated for species richness, Shannon diversity and species abundances. Then we compared them using linear mixed-effect models (LMM). The indicator species analysis was used to identify species typical for the under-canopy of shrub and for the adjacent open areas. The combination of stress factors affected the type and intensity of plant-plant interactions and plant life strategies (CSR) of the indicator species. *Artemisia kopetdaghensis* showed the highest facilitation effect under the most intensive stress conditions (high aridity/high grazing), which turned into competition under the low stress conditions (low aridity/low grazing). In the arid region, the canopy of shrub protected ruderal annual forbs and grasses with SR and R-strategy, respectively, in both high (high aridity/high grazing) and low grazing intensity (high aridity/low grazing). In the semi-arid region and high grazing intensity (low aridity/high grazing), the shrubs protected perennial forbs with C-strategy. Our FINDINGS highlight the importance of context-dependent shrub management in the restoration of vegetation damaged by intensive grazing.

Introduction

Species interactions are widely acknowledged as one of the most important drivers of the plant community structure, biodiversity, ecosystem function and dynamics (Callaway et al., 2005; Brooker et al., 2008; Jankju, 2013). However, the outcome of plant-plant interactions may vary, ranging from competition to facilitation, depending on environmental severity (Grime, 1977; Brooker & Callaghan, 1998) and on the character of coexisting species (Armas et al., 2011; Pugnaire et al., 2011). Interactions among plants may reduce the extreme abiotic and biotic stresses such as aridity (López et al., 2016) and intensive grazing (Smit et al., 2007 & 2009; Holmgren & Scheffer, 2010; Soliveres et al., 2011) by creating suitable micro-habitats for drought- or grazing-intolerant species (Bruno, Stachowicz & Bertness, 2003; Farzam & Ejtehad, 2017).

Grazing is essential biotic stress in dry rangelands due to its extensive application and potential contribution to variation of community structure, species composition, and degradation of ecosystem services (Li et al.,

2013, Díaz et al., 2007; Kéfi et al., 2007). Research in the ecosystems driven by large herbivores shows that unattractive, toxic or thorny plants may induce positive indirect (i.e., grazer mediated) effects on palatable herbs, shrubs or trees (Bakker et al., 2004; Callaway et al., 2005; Smit et al., 2006). Grazing may affect the outcome of plant-plant interactions as well, depending on the ability of the nurse plant to moderate the effects of herbivores and on the tolerance of the present species to herbivory (Baraza et al., 2006; Vandenberghe et al., 2009). Further, nurse plants may protect the neighbours against herbivory and enhance their recovery by increasing resource levels (Rand, 2004; Acuña-Rodríguez et al., 2006).

The CRS strategy, distinguishing between the competitors, ruderals and stress tolerators, provides a detailed view on the character of species typical for different types of vegetation, i. e. with varying intensity of environmental stress or grazing. The competitor, stress tolerator, and ruderal (CSR) theory (Grime 1979), based on the quantitative functional traits and life strategy, significantly improved the possibilities for analyzing ecological processes (Grime, 1977; Hodgson, Wilson, Hunt, Grime, & Thompson, 1999).

Previous researches have explored the effects of livestock grazing and climate on the relationships between plants (Metz & Tielbörger, 2016; Berdugo et al., 2018) but its effects on plant-plant interactions have rarely been addressed (but see Soliveres and others 2011, Verwijmeren et al., 2014; Filazzola et al., 2017). Moreover, the results of these studies are not consistent. For instance, Soliveres et al. (2011) showed that rabbit grazing caused positive interactions between the bunch grass (*Stipa tenacissima*) and saplings of the shrub (*Retama sphaerocarpa*) during winter and autumn. However, because of higher grazing intensity in the summer, the interspecific interactions shifted to neutral. Similarly, Holthuijzen and Veblen (2016) found that positive interactions between *Artemisia tridentata* ssp. *wyomingensis* and *Poa secunda* decreased with increasing grazing intensity in the arid region because grazing reduced productivity during the drought periods more intensively. This may result in the absence of positive interactions between plants due to different stressors (Smit and others 2009; Verwijmeren and others 2013; Michalet and others 2014). On the contrary, Noumi et al. (2016) showed that suppressive effects of shrubs on *Acacia tortilis* seedlings shifted to neutral with increasing grazing stress. Therefore, an increase in facilitation due to the combination of these two stressors can be expected. This research aimed at investigating the intensity of herbivore effect on plant-plant interactions when it is concurrent with drought. In addition, the CSR plant life strategies were used to interpret the inconsistency in the literature on changes in biotic plant interactions.

The selected dominant species, *Artemisia kopetdaghensis*, is an aromatic shrub that is widely distributed, ranging from warm and arid to cold and semi-arid steppes of northeast Iran (180-400 mm) and parts of Turkmenistan. We used *A. kopetdaghensis* and its understory plants as a model species to study the combined effects of grazing and climate (arid region: high/low grazing, semi-arid region: high/low grazing), aiming to answer the following questions: (i) What is the prevailing type of interaction between the dominant shrub *A. kopetdaghensis* and the surrounding understory herbs? (ii) Are the relations between *A. kopetdaghensis* and plants in its surroundings affected by aridity and intensive grazing? (iii) Do the effects of the shrub canopy vary according to the different plant life strategies under the combined effects of grazing and aridity?

Methods

Study area

We selected two regions along the precipitation gradient in northeastern Iran in the Khorassan-Kopet Dagh floristic province of the Irano-Turanian region, located between 35°43'-36°44'N and 58°40'-60deg27' E. Based on the meteorological data, Khaje has a dry climate and Baharkish has a semi-arid climate, expressed by de Martonne aridity index (see Table 1 for more details). The mean annual precipitation (20-year mean) is 255 mm in Khaje and 385 in Baharkish. A steppe vegetation with the dominant *A. kopetdaghensis* Krasch.M.Pop. & Linecz ex Poljak prevails in both of these areas. This species is a semi-shrub from the *Asteraceae* family, native to northeastern Iran and dominant throughout much of this region. *Artemisia* species have been documented to facilitate common annual and perennial forbs in this region (Reisner et al., 2015) by creating favorable suitable microsites, reducing evapotranspiration (e.g., Holthuijzen & Veblen, 2015), mediating soil temperatures (Davies et al., 2007), raising soil water content via hydraulic lift (e.g., Holthuijzen & Veblen,

2015) and accumulating soil nutrients (Cardon et al., 2013).

Sampling design

The two studied regions were 1600 ha and 1035 ha in size for the arid and semi-arid regions, respectively. The HG and LG sites were of similar size in both climatic regions. The distance between individual sampling areas within each climatic region was less than one kilometer, which is the least distance where we could identify plots with similar characteristics. The HG and pairwise LG sites were relatively homogenous in terms of topography, land use, and vegetation. The LG sites were located within fences that have prevented grazing for around 35 years, whereas HG sites were open and therefore have suffered long-term overgrazing. Each plot was characterized by geographic coordinates and altitude. In 2017, the number of individuals and percentage cover of all vascular plant species was recorded between April and June, when the growing season peaks in this region.

The decision about the grazing status of the sites (high grazing intensity vs. occasional/low intensity grazing) was based on the median number of dung droppings: 55.3 dung droppings per square meter in the HG and 6.2 in the LG sites, and also on the width of the microterrace livestock paths in a horizontal way (0.27+0.09 m for the HG site and 0.04+0.03 m for the LG site (see more information on the grazing history in Table 1).

The sampling design was arranged in a hierarchical way: In each of the two climatic regions (arid and semi-arid), we selected six sampling areas, with a high grazed and a low grazed site in each sampling area, arranged in a pairwise way (hereafter referred to as HG and LG sites). Then, we sampled three plots under the *A. kopetdaghensis* shrubs and three adjacent plots outside the canopy of *A. kopetdaghensis* (hereafter referred to as under-canopy and open plots) in each HG as well as LG site. Altogether, 144 plots were sampled: 2 climatic regions, 6 sampling areas in each climatic region, one pairwise HG and one LG site in each sampling area and 6 plots (3 under-canopy and 3 open) in each HG or LG sites (see Figure 1). We recorded the numbers of individuals of all vascular plant species and their percentage covers (as a proxy for biomass) and then calculated the Shannon index of species diversity ($H = -\sum_{i=1}^s p_i \ln p_i$) for each plot (Shannon, 1948); p_i is the proportion (n/N) of individuals of one particular species (n) divided by the total number of individuals (N), and s is the number of species.

To obtain comparable samples for assessing species richness in the surrounding ‘open’ plots (outside the canopy of *A. kopetdaghensis*), matching the size of each sampled *A. kopetdaghensis* canopy, we sampled at haphazardly selected paired points, located ~1 m away from the canopy edge of each sampled *A. kopetdaghensis* shrub. When the size of *A. kopetdaghensis* was not measured, a wire loop was shaped to match the size of the sampled *A. kopetdaghensis* canopy plot and then used to define the size of the patch sampled in the ‘open’ plot (Farzam & Ejtehadi, 2017). Again, all established plant abundance present on these open plots were recorded and identified to the species level.

Statistical analyses

Relative interaction intensity (RII) was used to assess the effect of shrubs on under-canopy vegetation (Armas et al., 2004) and was calculated based on the cover, richness, and diversity (expressed as Shannon index) of under-canopy vegetation: $RII = (\text{value under shrub} - \text{value in the open}) / (\text{value under shrub} + \text{value open})$. Samples were paired between each *A. kopetdaghensis* shrub and its neighbouring open plot. RII was used as an indicator of the facilitation by the target shrub, based on the performance of under-canopy plants. The interaction index has defined limits [-1,+1], with positive values indicating facilitation and negative values indicating competition.

The differences in RII indices for species richness, cover, and diversity between the HG and LG sites and between the arid and semi-arid regions were tested using the linear mixed-effect models, with “sampling areas” as a random effect, “climatic region” and “grazing” as fixed effects and RII based richness (RII-Richness), cover (RII-Cover), and Shannon H (RII-Shannon diversity) as response variables. All univariate analyses were performed in the R software, using the NLME package. The script for the model testing the

interaction between “climate” and “grazing” were “lme(Relative interaction intensity ~ climatic region * grazing, random = ~ 1 | sampling area)”. The normality of the input data was assessed based on Shapiro-Wilk tests, and the normality of residuals was checked visually, by plotting the observed values against the fitted values.

Further, we used the method of indicator species analysis to reveal the preference of individual species for the HG versus LG sites in both the arid and semi-arid climatic regions. With this approach, we could determine the indicator species sensitive or resistant to high grazing intensity in two different climatic regions. Indicator species analysis has two main components: (i) recorded on either HG or LG sites only (exclusivity); (ii) recorded on all samples of either the HG or LG group (fidelity). The indicator value index was assigned to all species, identifying species with the highest association values. The permutation tests (999 permutations) were used to estimate the statistical significance of individual species’ indicator values (Dufrene & Legendre, 1997). The indicator species analyses were performed using the “indicspecies” package of the R software (R Development Core Team, 2013).

We also calculated the values for CSR plant strategies for all indicator species as well as for *A. kopetdaghensis*, following Pierce et al. (2017), based on the following traits: specific leaf area (SLA), leaf dry matter content (LDMC) and leaf area (LA). We collected the leaves from robust and well-grown plants. Leaf material was collected from 10 individuals of each species, packed in moist paper bags, sealed in plastic bags, and stored in a thermal box until storage at 4 degC for 12–24 h. Depending on the size of leaves, 2–10 undamaged, fully expanded young leaves (including the petiole) were measured per individual. We determined the leaf area using a digital scanner and Leaf Area Measurement v1.3 software (Andrew Askew, University of Sheffield, UK). Turgid leaf fresh weight (LFW) was obtained from saturated leaves, and leaf dry weight was determined after drying for 72 h in an oven at 70 degC. For CSR strategy analysis, values of LA, SLA, and LDMC were inserted into the ‘StrateFy’ spreadsheet 3 to calculate C, S, and R percentages for each species (Pierce et al., 2017).

Results

The effect of climate and grazing interaction on plant-plant relations

We found significant effects of both grazing and aridity on the outcome of plant-plant interactions, expressed by the RII indices. In particular, the RII indices for species richness, abundances, and Shannon diversity were all positive in high aridity/high grazing conditions. The RII values were neutral (i.e. not significantly different from zero) for species richness and Shannon diversity in the low aridity/low grazing conditions and also for Shannon diversity in the low aridity/high grazing and even negative for RII-cover in low aridity/low grazing regime (Table 2).

Interaction intensity along the stress gradient

For all three indices (cover, richness, and Shannon diversity), RII was higher in the arid compared to the semi-arid climatic region (Figure 2). The RII indices for species’ cover, species’ richness and Shannon diversity were all positive on both the LG and HG sites in the arid region, indicating a facilitative effect of the target shrub, *Artemisia kopetdaghensis* (Figure 2; Appendix A). However, the response of RII to the grazing intensity varied with climatic conditions. A significant facilitation (expressed by the positive RII values) was recorded in the semi-arid region for species’ cover and richness, but only on the HG sites. The RII values for species’ covers were negative for the LG sites in the semi-arid region, indicating competition rather than facilitation by the dominant shrub (Figure 2; Appendix A). The RII values for Shannon diversity on the HG and LG sites in the semi-arid region and the RII values for species’ richness on the LG sites in the semi-arid region did not significantly differ from zero, indicating neutral interactions (Figure 2).

Plant strategies and Indicator species

The values of the C-S-R plant life strategies showed that *A. kopetdaghensis* was S-selected in all combinations of grazing and aridity levels. Stress-tolerant species were dominant under the shrub’s canopy in both the high-stress sites (high aridity/high grazing) and the low-stress sites (low aridity/low grazing), i.e. *Poa bulbosa* L., *Salsola dendroides* Pall., *Achillea biebersteini* Afan., and *Eremurus stenophyllus* (Boiss & Buhse)

Baker. However, the stress-tolerant species (S) were replaced by ruderals (R-selected, i.e. *Alyssum desertorum* Stapf, *Astragalus flicaulis* Kar. & Kir., *Callipeltis cucullaria* (L.) Stev., *Galium tricornerutum* Dandy) and competitors (C-selected, i.e. *Cirsium bornmuelleri* Sint. ex Bornm., *Prunus pseudoprostrata* (Pojark.) Rech.f, *Thalictrum sultanabadense* Stapf - Table 3), respectively, on the sites with intermediate stress levels: low intensity of livestock grazing or aridity (high aridity/low grazing and low aridity/high grazing).

Concerning the life cycle of indicator species, annuals prevailed on the LG sites. Perennials were present on the HG sites of the arid region and dominated in the semi-arid region, on both HG and LG sites (Table 3).

There were not many indicator species in the open plots, all of them annual/perennial stress-tolerant species (e.g. *Poa bulbosa* -HG sites in the arid region; *Aegilops triuncialis* and *Achillea bibersteinii* in LG sites of the semi-arid region- Table 3).

Discussion

Shrub canopy mediated abiotic and biotic stresses

Changes in relative interaction intensity (RII) indicate changes in interaction type along a combined gradient of biotic and abiotic stress. For all of the three RII indices (cover, richness, and Shannon diversity), there was a decreasing trend from the highest towards the lowest stress levels (Figure 2). The shrub (*A. kopetdaghensis*) showed facilitative effects, preserving species diversity and richness as well as the total cover of species under its canopy. However, the facilitative effect was significantly stronger in the drier climatic region. Previous researchers (Bertness & Callaway, 1994; Brooker & Callaghan, 1998; Butterfield, Bradford, Armas, Prieto & Pugnaire, 2016) have documented increases in the facilitation effect of the shrub by moderating the aridity stress. In arid environments, facilitation usually involves increasing the water and nutrient availability (Claus Holzzapfel & Mahall, 1999). Besides that, the shade from the shrub reduces extreme temperatures and decreases evaporation from the soil, which may further facilitate the germination of seeds and growth of seedlings. Therefore, this may explain why the shrub shows higher facilitation in the arid than in the semi-arid regions (Smit et al., 2007; Tirado et al., 2015; Farzam & Ejtehadi, 2017).

The effect of *A. kopetdaghensis* canopy was consistently facilitative under intensive grazing. As *A. kopetdaghensis* is unpalatable, it is not usually grazed by livestock during the growing season. Therefore, it provides mechanical refuge for palatable grasses and forbs (reviewed by Milchunas & Noy-Meir 2002; Baraza et al., 2006; Graff et al., 2007; Holthuijzen & Veblen, 2015). This result is consistent with the “repellent plant hypothesis”, suggesting that grazing intolerant plants are protected by the surrounding grazing tolerant plants (Milchunas and Noy-Meir 2002).

Relative interaction index along the stress gradients

Changes in type and/or intensity of plant-plant interaction along the stress gradients have been one of the most discussed issues in plant ecology in recent decades (Maestre, Callaway, Valladares, & Lortie, 2009). There are contrasting reports on this in literature, as some researchers conclude that the amelioration of abiotic stress was more important than protection from grazing (Howard et al., 2012; Arroyo et al., 2015). Other studies demonstrated that grazing was a more important driver of the plant-plant interactions than abiotic stress in the African savanna (Louthan et al., 2014; Filazzola et al., 2017).

In the arid region, strong facilitation was observed in both grazing intensities, which suggests that the protection against aridity is more important than protection from intensive grazing (Maestre et al., 2005; Soliveres et al., 2011). Accordingly, a theory by Smit et al. (2009) predicts relatively low importance of protection from grazing in water-limited environments. In arid climates, herbivores are sparsely distributed, and the availability of water or nutrients is more critical for vegetation than protection from grazing (Ellis & Swift, 1988). In water-limited environments, the shrubs usually improve soil fertility and microclimate under their canopies (Cortina & Maestre, 2005, Maestre et al., 2009). Also, shade from shrubs' and trees' canopy can retain soil moisture at the soil surface and facilitate neighbours with shallower roots (Maestre, Bautista & Cortina, 2003). Therefore, the dominant shrub may promote species richness and productivity by providing safe microsites for species growing in harsh conditions (Bruno et al., 2003).

On the other hand, in the semi-arid region, where plants presumably grow in higher water availability, livestock grazing played a critical role in determining the type and relative intensity of the shrub's interaction with under-canopy species. The effect of the shrub's canopy (RII) was positive on the HG sites, but turned into neutral or even negative with lower livestock grazing intensity. A negative RII means that herbs prefer to grow in the open areas rather than under the canopy of shrubs, where they need to compete for light, nutrients and water (Graff et al., 2007; Le Bagousse-Pinguet et al., 2012).

Indicator species response to plant interactions in the condition of stress

This study shows that co-occurring plant species under the shrub canopy may exhibit convergence in CSR plant life strategies in the conditions of similar levels of stress, while different stress levels lead to functional divergence. For instance, in the arid region, the dominant strategy of indicator species under *A. kopetdaghen-sis* converged to S-R in the HG site. At the same time, species under the shrub's canopy exhibited transition from S-R to R-selected in low grazing intensity. This is likely because important drivers of vegetation structure, such as disturbance (grazing) and stress (aridity), cause the loss of biomass and redistribution of resources (Caccianiga, Luzzaro, Pierce, Ceriani & Cerabolini, 2006), S-selected species prevail under the canopy of *Artemisia*. However, on the LG sites in the arid region, the canopy protects the surrounding plants from aridity only, so the stress is less intensive than on the HG site. Therefore, most of the indicator species under the shrub's canopy were annual forbs and grasses with R strategy on the LG site. Plants with R-selected strategy absorb nutrients more rapidly, grow faster, have shorter growth periods and invest more into reproduction (Grime, 1977; Caccianiga et al., 2006; Wang et al., 2018). Stress intolerant species were better candidates for facilitation than stress-tolerant species (Graff & Aguiar 2011). For instance, in the arid conditions of Mediterranean shrublands, the stress avoidant species, with high specific leaf area and rapid growth, coexist with species featured by very low specific leaf area (Gross et al., 2013).

In the semi-arid region, *A. kopetdaghen-sis* canopy showed a facilitative effect on the HG sites, supporting the establishment of species with C-selected strategy, like *Elymus hispidus* or *Lactuca orientalis*, which have larger leaves and are generally more palatable to livestock. This is mainly because *A. kopetdaghen-sis* is an unpalatable, stress-tolerant shrub, and its canopy creates microsites, protecting other species against grazing by large herbivores. In contrast, *A. kopetdaghen-sis* canopy has a competitive or neutral effect on the perennial stress-tolerant species on the LG sites in the semi-arid region. *A. kopetdaghen-sis* shrubs have a neutral effect or even compete with the under-storey species for light and nutrients. Therefore, the dominant strategy of indicator species under *A. kopetdaghen-sis* in HG site shifted from C- to S-selected in LG site.

On the contrary, we found only a few indicator species in the open plots in both the arid and semi-arid regions. *Poa bulbosa* was present in the HG sites of the arid region, *Aegilops triuncialis* and *Achillea biber-esteinii* were on the LG sites of the semi-arid region (Table 3). As suggested by Grime (1977), when the disturbance is relatively low, species with S-strategy can maintain their dominance in a community by occupying aboveground and belowground space rather than by competing for resources.

Conclusions

Our results document that local-scale biotic processes, such as facilitation by the shrubs, are important determinants of diversity patterns. In general, shrubs are known to provide refuge for species in harsh conditions, such as high aridity or overgrazing. Furthermore, we argue that the discrepancy in the literature on changes in plant-plant interactions may be partially explained by differences in plant life strategies of species in the conditions of the combined effect of biotic (grazing) and abiotic (aridity) stress. Therefore, in the arid region, drought-escaping species like ephemerals and ruderals (R-selected) and species tolerating stress (S-selected) but avoiding herbivory are highly dependent on the facilitation under the canopy of shrubs. However, in sites without severe aridity, canopy of the target shrub protected competitive species (C-selected) in the conditions of high grazing intensity (low aridity/high grazing). On the contrary, on sites without intensive grazing and severe aridity (low aridity/low grazing), facilitative effects of the shrub turned to neutral or even competitive.

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Conflict of interest

None declared.

Author contributions

H.E, M.F and F.M designed the study. S.R collected the data, performed the analysis and wrote the manuscript. M.H and M.F contributed to the interpretation of the results and work on the manuscript. F.M and P.P Commented on the manuscript. All authors contributed to different versions of the manuscript and discussed the results and gave final approval for its publication.

Data accessibility

Data will be made available in the Dryad Digital Repository

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TABLE 1 Basic characteristics and grazing history of the arid and semi-arid regions in northeastern Iran.

Region	Khawjeh Kalat 35° 43'- 35° 50' N, 60° 27' - 60° 34' E	Khawjeh Kalat 35° 43'- 35° 50' N, 60° 27' - 60° 34' E	Baharkish 36° 44' - 36° 42' N, 58° 40' - 58° 36' E	Baharkish 36° 44' - 36° 42' N, 58° 40' - 58° 36' E
Climate classification (De Martonne)	Arid	Arid	Semi-arid	Semi-arid
Mean annual precipitation (mm)	255	255	385	385
Mean annual temperature	17.9	17.9	13	13
De Martonne Index	9	9	15.5	15.5
Elevation (m)	630-810	630-810	1580-2390	1580-2390
Management	Grazing area	Area protected from grazing	Grazing area	Area protected from grazing
Grazing history	Seasonal- free ranging	protected in the last 35 years, occasional light grazing in some years	Seasonal- free ranging	Protected in the last 35 years, occasional light grazing in some years
Grazing type	Seasonal, 20 March - 10 May	Seasonal, 20 March - 10 May	Seasonal, 20 May - 23 July	Seasonal, 20 May - 23 July
Grazers type	Sheep (90%), goat (10%)	Sheep (90%), goat (10%)	Sheep (90%), Goat (10%)	Sheep (90%), goat (10%)
Grazers density	3 AUM/ha	0-0.5 AUM/ha	2 AUM/ha	0-0.5 AUM/ha

AUM: Animal Unit Month

Table 2 Results of linear mixed-effect models, testing the effects of climate, grazing, and their interactions on RII.Shannon, RII.Richness and RII.Cover.

	Climate	Climate	Climate	Grazing	Grazing	Grazing	Climate × grazing	Climate × grazing
	df	F	p	df	F	p	df	F
RII-Cover	1	17.46	<.001***	1	13	0.0006***	2	15.6
RII-Richness	1	9.56	0.01**	1	5.07	0.02*	2	4.88
RII-Shannon	1	7	0.02*	1	3.62	0.06	2	3.87

*** $p < .001$, ** $p < .01$, * $p < .05$, no asterisk ($p < .1$)

TABLE 3 List of indicator species found under *A. kopetdaghensis* canopy and on open plots of the HG and LG sites in the arid and semi-arid regions, showing the exclusivity and fidelity of indicator species. Significances refer to indicator values (exclusivity × fidelity) (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, permutations = 999).

Species of the under-canopy plots	Semi-arid LG	Semi-arid HG	Arid-LG	Arid-HG	Life cycle
<i>Achillea biebersteini</i> Afan.	0.045*				A
<i>Alyssum desertorum</i> Stapf			0.002**		A
<i>Astragalus (Caprini) citrinus</i> Bunge		0.01*			P
<i>Astragalus flicaulis</i> Kar. & Kir.			0.002**		A
<i>Astragalus oxyglottis</i> M.Bieb.		0.01*			A
<i>Bromus danthoniae</i> Trin.			0.03*		A
<i>Bromus tectorum</i> L.	0.005**				A
<i>Callipeltis cucullaria</i> (L.) Stev.			0.04*		A
<i>Cirsium bornmuelleri</i> Sint. ex Bornm.		0.01*			P
<i>Elymus hispidus</i> (Opiz) Melderi		0.001***			P
<i>Eremurus stenophyllus</i> (Boiss & Buhse) Baker	0.005**				P
<i>Galium tricornutum</i> Dandy			0.001***		A
<i>Lactuca orientalis</i> Boiss.	0.046*				P
<i>Poa bulbosa</i> L.				0.006**	P
<i>Prunus pseudoprostrata</i> (Pojark.) Rech.f		0.01*			P
<i>Salsola dendroides</i> Pall.				0.01*	P
<i>Thalictrum sultanabadense</i> Stapf		0.005**			P
Species of the open plots	Semi-arid LG	Semi-arid HG	Arid LG	Arid HG	Life cycle
<i>Achillea biebersteini</i> Afan.	0.04*				A
<i>Aegilops triuncialis</i> L.	0.004**				A
<i>Poa bulbosa</i> L.				0.01*	P

Abbreviations of the C-S-R plant life strategies: C: competitive, S: stress tolerating, R: ruderal. Abbreviations of the life cycle: A: annual, P: perennial

Figure legends

Figure 1. a) Map of the study area in NE Iran, showing the Khajeh Kalat as an arid region, with ~255 mm of annual precipitation and Baharkish rangeland as a semi-arid region, with ~385 mm of annual precipitation, b) Natural habitat with *Artemisia kopetdaghensis* as a dominant species, c) Plant communities around *Artemisia kopetdaghensis*, the arrows point to other species under the canopy of *A. kopetdaghensis*

Figure 2. Comparisons of relative interaction indices (RII-Richness, RII-cover, and RII- Shannon diversity) of *A. kopetdaghensis* between the HG and LG sites in the arid and semi-arid regions.

Appendices

Appendix A. Mean values of the relative interaction intensity (RII), corresponding to the relative effect of the canopy of *Artemisia kopetdaghensis* on the under-canopy communities.

Climatic region	Grazing	RII-Richness	RII-Cover	RII-Shannon diversity
Arid	HG	0.2	0.33	0.16
	LG	0.19	0.26	0.18
Semi-arid	HG	0.18	0.3	0.01
	LG	-0.14	-0.38	-0.11

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