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Effects of drought and slope aspect on canopy facilitation in a mountainous rangeland

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Abstract

Aims

Species composition and diversity of the mountainous rangelands are results of interactions between environmental severities, heterogeneous topography and facilitative effects by nurse plants. This research was aimed to compare relative effects of these three environmental variables on the natural vegetation of a mountainous rangeland. For a more detailed understanding, effects of four different nurse species were separately compared on the various plant growth forms and on two community plant responses (diversity and abundance).

Methods

A mountainous semiarid rangeland was selected in Baharkish, Quchan, Northeast of Iran. Density and canopy cover of all plant species were recorded under the canopy of four different shrubs and in open areas, in north and south-facing aspects, and in a normal and a drought year. Shannon diversity, total abundance (% cover) and the abundance of different growth forms were used as criteria for assessing effects of the environmental variables. Data were arranged in a factorial combination and analyzed by three-way analysis of variance using a GLM analysis.

Important Findings

(i) Drought, aspect and canopy created niche differentiation: annual forbs and shrubs were more affected by drought, whereas geophytes and grasses were more responsive to slope aspects. Effects of drought and slope aspect were more profound on species diversity, whereas that of canopy facilitation was stronger on plant abundance. (ii) Canopy facilitation was dependent on severity of the abiotic factors and life history of interacting species. Canopy facilitation allowed for the persistence of only annual forbs, but it was disadvantaged during the drought year. Plant community responses to abiotic factors (slope and drought) were more dependent on the plant growth form, while responses to canopy facilitation were more dependent on the morphology and/or ecology of nurse shrubs. (iii) Effect of shrubs was dependent on their morphology and ecology: shrubs with larger canopy area and nitrogen fixation capability increased, but those with allelopathic effects or a dense canopy structure decreased the diversity of the understory species.

Keywords: biotic interactions, facilitation, slope aspect, plant ecology, growth forms

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INTRODUCTION

Species diversity and abundance of semiarid vegetation are outcome of interactions between several biotic and abiotic environmental factors. Effect of each factor may be influenced by the extent and availability of other variables. Many studies from harsh environments report higher fertility under shrubs, measured as improved plant survival, fecundity, biomass or density (e.g. Greenlee and Callaway 1996; Madrigal-González *et al.* 2015; Shumway 2000; Tielbörger and Kadmon 2000; Yu *et al.* 2008). Moreover, higher species richness and diversity have repeatedly been found under shrubs canopy than their adjacent open areas (e.g. Castro *et al.* 2002; Lindh *et al.* 2014; Tewksbury and Lloyd 2001). However, the facilitation effects of shrubs on their understory vegetation may be affected by site topography (e.g. Bertness and Ewanchuk 2002; Garcia *et al.* 2007) and annual rainfall (Brooker *et al.* 2008; Deleglise *et al.* 2015; Madrigal-González *et al.* 2015; Maestre and Cortina 2004). Some studies suggest that shrub-nursing effects may increase species richness during dry years, but not wet years (Garcia-Fayos and Gasque 2002; Pugnaire and Lazaro 2000), whereas more recent studies (e.g. Jankju 2013; Soliveres *et al.* 2013; Zhang *et al.* 2015) suggest negative effects of shrubs during drought conditions. Accordingly, further research is appealed to compare relative (positive or negative) effects of shrubs on their understory plants during wet and dry years.

A combination of environmental severity, heterogeneous topography, and the relatively high frequency of potential nurse plants make the mountainous rangelands a suitable system for studying the facilitative effects of nurse plants over small spatial scales (Alejandro *et al.* 2009). In mountainous areas of the northern hemisphere, the benign conditions in mesic slope (northern) aspects support more productive and fragile plant species, whereas harsher conditions in drier (southern) aspects leads to the establishment of more stress-tolerant species such as cacti and spiny shrubs (Badano *et al.* 2005; Bennie *et al.* 2006; Gong *et al.* 2008; Yu *et al.* 2008). Therefore, shrubs may show higher facilitation effects in xeric rather than mesic exposures (e.g. Alejandro *et al.* 2009; Badano *et al.* 2005; Garcia *et al.* 2007). Similarly, changes in the total annual rainfall (i.e. drought versus wet years) can also provide xeric or mesic conditions. Therefore, studying interaction between effects of slope aspect and annual precipitation is needed for an improved understanding on the effects of shrubs on diversity and abundance of the mountain rangelands.

Plant community responses to environmental conditions (e.g. drought, salinity and cold stresses) are also dependent on the growth forms (Ehleringer *et al.* 1999), and life strategies (Grime 2001) of plant species. Several studies have also shown significant effects of life history (Maestre *et al.* 2009; Michalet *et al.* 2006) and taxa relatedness (Valiente-Banuet and Verdú 2008) of the interacting plants on the outcome of plant-plant interactions. Therefore, in his research, we distinguished between the type of plant responses to the environmental variables, by separately comparing effects of environmental factors on species diversity and abundance; also their impacts were separately compared on different plant life forms (annual grasses, annual forbs, geophytes, perennial grasses, perennial forbs and shrubs).

There are numerous reports in the literature (e.g. above mentioned references) for the effects of drought, slope aspect and canopy facilitation on the plant species diversity and abundance. However, studying these factors in a single study and interpretation of their effect in relationship with the life history of interacting species has rarely been considered. Accordingly, this research was aimed to investigate the main effects and interactions between physiography (slope aspect), climate (normal or dry year) and canopy facilitation (presence of nurse shrubs) on the plant diversity and abundance in a semiarid mountainous rangeland.

MATERIALS AND METHODS

Study area

This study was conducted in a semiarid rangeland, Baharkish, Quchan, northeast of Iran. Latitude and longitude were 36°42′N and 58°37′E, respectively. The study was conducted within the northern or southern slope aspects of a single mountain, during two consecutive years. Average elevations of the northern and southern sites were, respectively, 2347 and 2376 meters above the sea level (m.a.s.l.), with the sampling area of each site being about 20 000 m^2 (100×200 m). Both study sites had been under similar grazing intensity by livestock (sheep and goat), our field measurements were conducted just before the beginning of the grazing season (15–20 of May) in 2013 and 2014. The climate of Baharkish is classified as semiarid Mediterranean, according to the Emberger's classification method, which represents cold and wet winters, mild and dry summers. Mean annual rainfall (20 years data) is 354.4 mm that mainly occurs as snowfall during November through May. About 88% of total annual rainfall occurs before mid-May (October–May) and only 12% occurs for the remaining months (mid-May–September) (Khaksarzadeh, 2014) Annual rainfall in 2013 was 322.4 mm, but it severely (63%) decreased to 122 mm in 2014. Average maximum daily temperature in July is 31.4 and minimum daily temperature in January is −7°C. Climate data were obtained from Bar Climatology Station, 10 km from the studied sites. Growth season starts at early April and ends at late July (for annuals and perennial herbs), but some shrubs continue growth till early-November.

Effect and response parameters

Effects of major environmental factors were assessed on vegetation cover and species diversity of Baharkish rangelands. The first environmental factor was a severe reduction in annual rainfall (63%) from the normal (2013) to the dry (2014) year. The second factor was the effect of north versus south-facing slopes of a single mountain. As the third factor, we analyzed effects of nurse shrubs compared to adjacent open areas. Moreover, effects of four particular nurse shrubs were compared, *Astragalus meschedensis* Bunge, *Acanthophyllum glandulosum* Bunge ex Boiss., *Acantholimon* sp., and *Artemisia khorassanica* Podl, which differed in terms of morphology and ecological traits. *Astragalus* and *Artemisia* had a more porous canopy and a brighter understory, whereas *Acantholimon* and *Acanthophyllum* had dense cushion-like canopy structures. *Astragalus* had the greatest (about 1×1 m diameter on average), whereas *Artemisia* had the smallest (0.5×0.5 m) canopy area. *Astragalus* is a legume species with possible nitrogen fixation capability, whereas *Artemisia* is an allelopathic shrub (Behdad *et al.* 2011).

Vegetation sampling

Vegetation cover of each slope aspect was sampled by using 50 quadrates, with 10 replicates randomly designated to five microsites (i.e. understory of four nurse shrubs and in open areas). To avoid pseudo-replication, plant sampling was conducted at three different sites at high, intermediate and low altitudes of each slope aspects, pretending three separate blocks. Sampling was conducted twice, summer 2013 and summer 2014, on the same sites. For measuring plant abundance, percent cover of each plant species was measured separately within 1 m^2 quadrates. In each quadrate, the scientific name, growth form, canopy area and density of all plant species were recorded. Canopy area of perennial plant species was calculated by measuring their longest dimensions (width and length). For annuals, canopy area of few samples (5–10) were exactly measured and averaged, then multiplied by their total number within each quadrate.

Data analysis

A full factorial combination of two annual rainfall levels, two slope aspects and five microsites resulted in 20 environmental conditions, with the number of replicates being 10, the total quadrate number becoming 200. Three-way analysis of variance (ANOVA) was applied on the data using Generalized Linear Modeling (GLM analysis) in SPSS 16 software. Main effects and interaction between the environmental factors were tested on three vegetation attributes: Shannon–Weiner diversity index (Shannon diversity), abundance (% cover) of each plant growth form (annual forbs, annual grasses, perennial forbs, perennial grasses, geophytes and shrubs), and total abundance (% canopy cover) per square meter. Shannon diversity was estimated using Biodiversity Pro (McAleece *et al.* 1997) and Ecological Methodology (Kenny and Krebs, 2001) programs. Wherever effects of environmental factors were significant ($P < 0.05$), *post hoc* analyses were conducted on mean data of species diversity or % cover, by using a Tukey test.

RESULTS

Here, we have presented effects of three major environmental factors i.e. drought, slope aspect and shrub canopies (effect parameters) on plant abundance and diversity (response parameters), in the mountainous rangelands of Baharkish. First, simple effects of the environmental factors are illustrated on the abundance (canopy cover) of different plant growth forms (Fig. 1a–c). Second, total vegetation cover (abundance) and species diversity are compared under the canopy of four rangeland shrubs (*Acantholimon*, *Acanthophyllum*, *Astragalus* and *Artemisia*) and in open areas (Fig. 2a and b). Results of a three-way ANOVA are also shown for the effects of drought, slope aspect and their interactions on the Shannon diversity index (Table 1). Finally, we have illustrated, the way drought and/or slope aspect may affect canopy facilitation of shrub species on their understory plants (Fig. 3a and b).

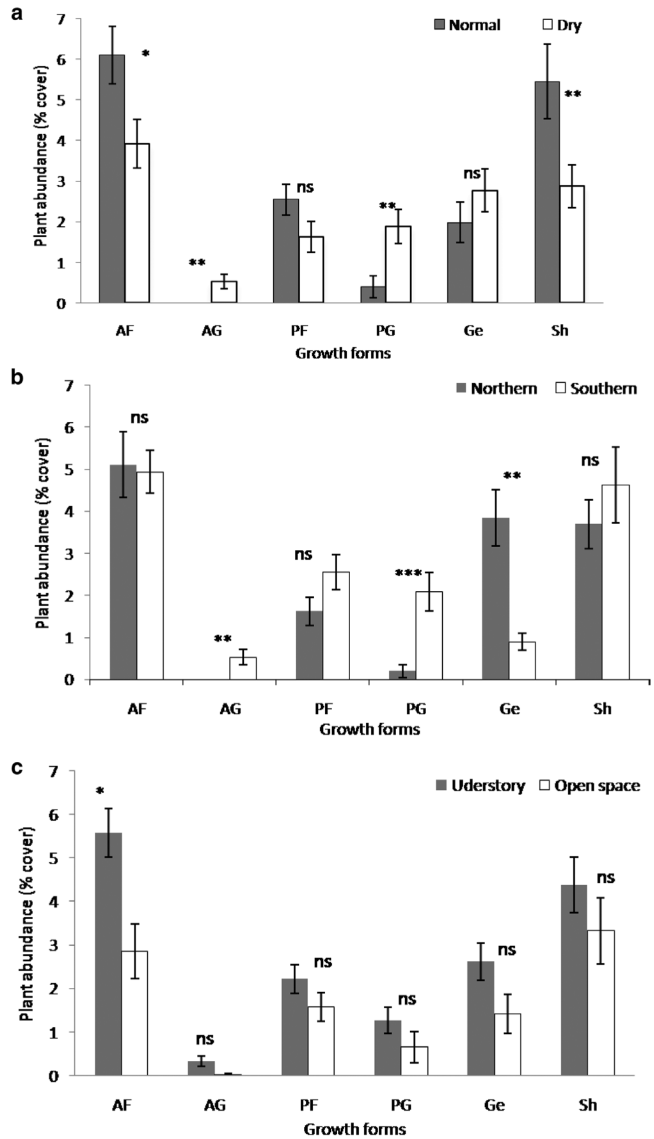

Figure 1: effects of the three main environmental variables, drought (**a**), slope aspect (**b**), and shrub canopies (**c**), on Shannon diversity index. Abbreviations: AF = annual forbs, AG = annual grasses, Ge = geophytes, ns, non-significant, PF = perennial forbs, PG = perennial grasses, Sh = shrubs. * , ** and *** = significant at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

Effects of drought

Abundance of different growth forms were compared between the dry and normal year (Fig. 1a). Drought significantly reduced the abundance of annual forbs and shrubs, but that of annual and perennial grasses were higher in dry than normal year. Abundance of perennial forbs and geophytes did not vary between the years (Fig. 1a).

Analysis of variation showed significant effects ($P < 0.001$) of drought on species diversity (Table 1), with the Shannon diversity index being significantly lower during dry than normal year (data not shown).

Effects of slope aspect

Abundance of different growth forms were compared between the northern and southern slopes of Baharkish rangelands (Fig. 1b). Annual and perennial grasses were more abundant on the southern slope, whereas geophytes were more common on the northern slope. Percent cover of annual and perennial forbs and shrubs did not significantly vary between north and south slope aspects.

Analysis of variation revealed significant effect ($P < 0.05$) of slope aspect on species diversity (Table 1), with the Shannon diversity index being significantly higher in south than north-facing slope (data not shown).

Effects of shrubs' canopy

Abundance (percent canopy cover) of various plant growth forms were compared between the understory of shrubs and the open areas (Fig. 1c). Accordingly, annual forbs were more abundant under the canopy of shrubs than in open areas, but other growth forms (annual grasses, perennial forbs, perennial grasses, and shrubs) were similarly found under the shrub species and in open areas (Fig. 1c).

Vegetation abundance (sum of the canopy cover of all growth forms) was compared for plants growing under the canopy of various shrub species and/or in open areas (Fig. 2a). It was significantly higher under the canopy of *Artemisia* and *Astragalus;* which may indicate higher capability for these species as compared with the open areas or understory of *Acantholimon* and *Acanthophyllum* species.

A comparison of Shannon species diversity (Fig. 2b) revealed the highest and lowest values under the canopy of *Astragalus* and *Artemisia*, respectively, with intermediate being found for diversity index the canopy of *Acantholimon*, *Acanthophyllum* and in open areas.

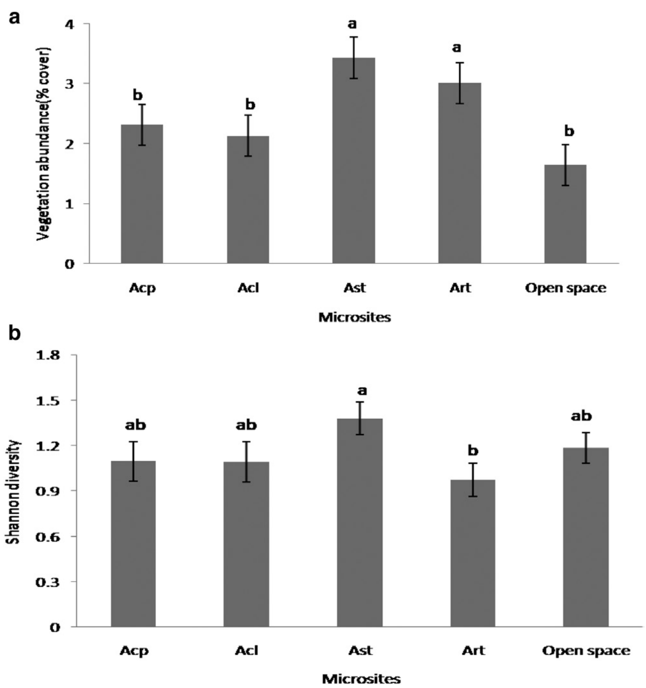

Figure 2: general effects of drought and slope aspect (**a**), and shrub canopies (**b**) on the Shannon diversity index. Abbreviations: Acp = *Acanthophyllum*, Acl = *Acantholimon*, Ast = *Astragalus*, Art = *Artemisia*. Means indicated by a and b are significantly different at $P < 0.05$.

Canopy effects in dry or normal year

Interaction between effects of shrub canopy and drought was significant ($P = 0.006$) on the species diversity (Table 1), which indicates different effects of shrubs during dry or normal year. Drought reduced Shannon diversity for plants growing under the canopy of *Acantholimon* and *Acanthophyllum* and those in open areas, whereas it did not significantly affect those growing under the canopy of *Astragalus* and *Artemisia*. In other words, plants growing under the canopy of *Astragalus* and *Artemisia* were efficiently preserved but those growing under the canopy of cushion-like (*Acanthophyllum* and *Acantholimon*) species or in open areas were highly affected by drought stress (Fig. 3a).

Canopy effect in northern or southern slopes

Interaction between effects of shrub canopy and slope aspect was significant ($P = 0.028$) on species diversity (Table 1). This indicates different effects of shrubs on their understory plants, when they were growing in the north or south-facing slopes (Fig. 3b). For *Artemisia* understory, species diversity was higher in the north than south-facing slope. In contrast, in the open areas, plant diversity was higher in the south-facing slope (Fig. 3b). For the other three shrubs (*Acanthophyllum*, *Acantholimon* and *Astragalus*) understory species diversity

Table 1: three-way analysis of variance for the main effects and interaction between effects of drought, slope aspect and shrub canopies on the Shannon diversity index

Source	Type III sum of squares	df	Mean square	*F* value	Significance
Intercept	258.063	1	258.063	637.193	0.000
Drought	17.967	1	17.967	44.363	0.000
Aspect	1.974	1	1.974	4.8743	0.030
Canopy	3.680	4	0.920	2.272	0.066
Drought × aspect	0.306	1	0.306	0.756	0.389
Drought × canopy	6.167	4	1.542	3.807	0.006
Aspect × canopy	4.556	4	1.139	2.812	0.028
Drought × aspect × canopy	0.989	4	0.247	0.610	0.661
Error	72.977	180	0.405		
Total	368.760	200			

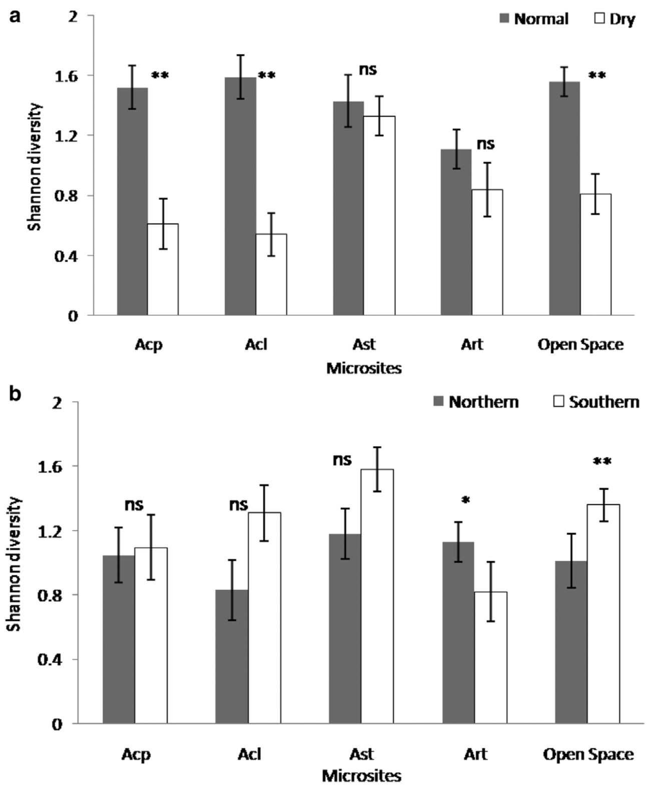

Figure 3: total vegetation abundance (%cover) under canopy of different nurse shrubs or in open areas. Abbreviations: Acp = *Acanthophyllum*, Acl = *Acantholimon*, Ast = *Astragalus*, Art = *Artemisia*. * , ** and *** = significant at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

did not vary, whether they were growing in the north or in south-facing slopes (Fig. 3b).

DISCUSSION

A simultaneous study on the effects of drought, slope aspect, and canopy of four different shrubs, on species diversity and abundance of different plant growth forms, enabled us to differentiate between effects of abiotic (drought and slope aspect) and biotic (shrub canopies) factors. Further, we could differentiate between responses of different plant growth forms to the main environmental variables, by doing separate analyses on their abundances. Although we had chosen the comparable sites in terms of rangeland management, however some environmental factors, which have not been studied in this research, such as soil depth, soil fertility, and wildfire burning may have had significant effects on niche differentiation of different plant growth forms in our study sites (e.g. El-Amier 2016). Therefore, we are percussive on generalizing the results for other ecosystems, except the comparable mountainous rangelands.

Drought, aspect and canopy created niche differentiation

Effects of drought and slope aspect (i.e. abiotic factors) were more profound on species diversity than on total abundance (Table 1 and Table 2). Studies by Pugnaire and Lazaro (2000) and Madrigal-González *et al.* 2015 also showed that rainfall availability strongly affected the community composition of understory, whereas the canopy effect was only an important sorting factor for the presence of individual species. Therefore, higher effect of drought and slope aspect (the abiotic factors) on species diversity, than abundance, indicates their importance for niche differentiations of plant species in the mountainous rangelands.

Results on plant abundance also indicate niche differentiation between the plant functional types (e.g. Ehleringer *et al.* 1999), in which each group of plants show the greatest performance (germination, establishment and/or growth) under the specific environmental conditions. Geophytes were mainly growing in the northern slopes, grasses were more abundant in the southern slope, but annual forbs, perennial forbs and shrubs were similarly distributed between the two slope aspects. Annual forbs were mainly grown under canopy of shrubs, whereas all other growth forms were evenly distributed under canopy and in open areas. Such habitat differentiation may increase the community stability and resilience against biotic (e.g. grazing, competition, allelopathy) and abiotic (e.g. drought, wildfire, temperature fluctuations) environmental factors (Ehleringer *et al.* 1999; Jankju 2008).

The significant effects of rainfall and slope aspects on species diversity can be due to differences in moisture (Neuner *et al.* 1999; Pake and Venables, 1996; Pugnaire and Lazaro 2000) and temperature (Neuner *et al.* 1999; Gong *et al.* 2008) thresholds for germination and establishment of individual plant species. Therefore, higher abundance of geophyte species in the northern slope aspect and higher presence of grasses in the southern aspect may, respectively, be related to their lower and higher threshold for air temperature and soil moisture. For shrubs and perennial forbs, sum of canopy cover of all species were similar between northern and southern slopes. Nevertheless, dry tolerant shrubs such as *Astragalus meshedensis*, *Artemisia kopetdaghensis* and perennial forbs such as *Teucrium polium* and *Peganum harmala* were more frequent in the southern aspect, whereas cold tolerant and mesophyte shrubs such a *Acantholimon* spp, *Onobrychis cornuta* and perennial forbs such as *Ziziphora clinopodioides* and *Alyssum* spp were more abundant in the northern slope aspect. Therefore, perennial forbs and shrubs well responded to the slope aspect, despite of having similar abundance (total canopy cover) in the southern and northern slope aspects.

Responses to drought were dependent on the ecological niches

Abundance of annual forbs and shrubs were significantly reduced, perennial grasses increased, but geophytes and perennial forbs remained unchanged, in response to the drought effect. Contrasting responses to the increasing temporal severity of drought might be due to the differences in life history of the plant species that were growing in the north and south-facing aspects. In the northern hemisphere, south-facing

Table 2: summary of three-way analysis of variance (only mean of squares and *P* values are shown) for the effects of year, slope aspect, shrub canopies, and interaction between them on the abundance total plants (all) and those of different plant growth forms

Variables	All	AF	AG	PF	PG	Ge	Sh
Drought	444.02^{ns}	288.87*	15.79**	31.08^{ns}	86.85**	32.00^{ns}	399.47**
Aspect	50.00^{ns}	1.55^{ns}	15.79**	53.71^{ns}	147.00***	423.17***	20.78^{ns}
Canopy	721.74**	98.75*	2.310^{ns}	30.75^{ns}	15.49^{ns}	25.56^{ns}	61.27^{ns}
Drought × aspect	62.72^{ns}	15.82^{ns}	15.79**	26.56^{ns}	42.43*	109.67*	97.78^{ns}
Drought × canopy	51.61^{ns}	116.47*	2.31*	0.76^{ns}	12.00^{ns}	37.69^{ns}	124.94*
Canopy × aspect	170.27^{ns}	46.09^{ns}	2.31^{ns}	21.68^{ns}	10.67^{ns}	21.09^{ns}	161.20*
Canopy × aspect × drought	145.46^{ns}	38.39^{ns}	2.31^{ns}	16.94^{ns}	3.67^{ns}	5.43^{ns}	126.20*

Abbreviation: AF = annual forbs, AG = annual grasses, Ge = geophytes, ns, non-significant, PF = perennial forbs, PG = perennial grasses, Sh = shrubs.
*Significant at $P < 0.05$, **significant at $P < 0.01$, ***significant at $P < 0.001$.

slopes generally experience higher temperature, greater light intensity, and lower moisture availability than north-facing slopes (Small and McCarthy 2002), thereby resulting in the aspect-related gradient on humidity, soil moisture and both soil and air temperatures (see also Badano *et al.* 2005; Gong *et al.* 2008). Previous research (e.g., Bennie *et al.* 2006) has also shown that south-facing slopes usually maintain more stress-tolerant or drought-escaping species, whereas more mesic sites of northern slopes are usually composed of fragile plant species that are more sensitive to drought effects. The Mediterranean type matorral of Central Chile which have equatorial-facing slopes were xeric and dominated by spiny shrubs and cacti, while evergreen sclerophyllous trees dominated polar-facing slopes due to their mesic conditions (Badano *et al.* 2005). In this research, drought had no effect on annual grasses and perennial grasses, i.e. life forms that were growing in the xeric sites of southern slopes. Furthermore, a release from competitive effects of other plant species may also be an alternative reason, for higher abundance of grasses during the dry year.

Drought had the greatest effects on annual forbs and shrubs. On the other hand, forbs were the most abundant growth form under the canopy of shrubs. Therefore, in the drought year, high competition for soil moisture between the overstory (shrubs) and understory (forbs) plants, may have led to high mortality of both growth forms. Previous studies by Jankju (2013) indicated facilitation effects of rangelands shrubs for establishment of a perennial forage grass in a normal year, which turned into high-competition effects and seedling mortality during the dry growth season, in the steppe rangelands of Karnakh, Iran. Zhang *et al.* (2015) also referred the intense competition between a shrub, *Nitraria sphaerocarpa* and its understory annuals to moisture reduction, in the deserts of northeast China. Another study in Spain (Soliveres *et al.* 2013) revealed the negative impact of understory herbaceous species on the juveniles of *N. sphaerocarpa*, when they were competing for soil moisture. Therefore, results of these research verifies the intense interaction between shrubs and their understory annuals, which may lead to high mortality of both species under the harsh climatic conditions.

Response of different growth forms to drought may also indicate a possible response of ecosystem to future climate change. Accordingly, drier climatic conditions in this region, as is anticipated by climate change models (e.g. Jackson *et al.* 2001), may lead to an invasion of annual and perennial grasses at the expense of annual forbs and shrubs which are the most and least-adapted plant species to drought conditions, respectively.

Effect of shrubs was dependent on their morphology and ecology

Rangeland shrubs affected both species diversity and total abundance of understory plants, but their facilitation effect was stronger on plant abundance (Fig. 2). The non-significant effect of canopy on species diversity can be due to two different reasons (i) different nurse shrubs provide contrasting microclimate conditions under their canopy and (ii) plant growth forms respond differently to the microclimate conditions under the canopy of each shrub species; the issues discussed in the following paragraphs.

Effects of nurse shrubs on their understory plants are highly dependent on morphology and/or ecological traits (Brooker *et al.* 2008). Pugnaire and Lazaro (2000) and McKenzie *et al.* (2000) found higher benefits from shrubs with larger canopy sizes. Therefore, in our research, the highest plant abundance under the canopy of *Astragalus* than under other nurse shrubs could be due to its greater canopy area. In a study in Baharkish area, Jankju *et al.* (2008) found higher soil fertility under the canopy of *Astragalus*, *Acantholimon* and *Acanthophyllum* as compared with those of *Artemisia* and open areas. They referred this difference to higher litter accumulation under canopy of cushion-like nurse species and a possible nitrogen fixation capability by *Astragalus* as a Leguminosae species (e.g. Alpert and Mooney 1996; Chapin *et al.* 1994).

The dense cushion-like *Acantholimon* and *Acanthophyllum* species did not cause any negative or positive effects on the abundance of their understory species, as compared with those growing in open areas. Even a higher soil fertility under the cushion-like nurse shrubs (Jankju *et al.* 2008) did not led to higher species abundance, possibly because of negative effects of litter accumulation and lower light availability. Light-shielding effects together with the presence of deep litter accumulation have been shown to play a negative role in seedling regeneration (Xiong and Nilsson 1999; Yu *et al.* 2008) and species richness and diversity (Madrigal-González *et al.* 2015; Rodriguez-Echeverria and Perez-Fernandez, 2003) of understory plants. Therefore, a balance between positive effects of higher soil fertility and negative effects of thick canopy structure could be the reason for non-significant effects of cushion shrubs on the species diversity and abundance of their understory plants.

Artemisia showed contrasting effects: it positively increased the total abundance but negatively reduced the diversity of plant species under the canopy. In a study by Jankju *et al.* (2008) in the Baharkish rangelands, higher soil moisture, lower irradiation and milder air temperature were found under canopy of *Artemisia* compared to open areas. In the same areas and for the same species, Behdad *et al.* (2011) found allelopathic effects of *Artemisia* on seed germination and seedling growth of *Bromus kopetdaghensis*. Therefore, favourable microclimate conditions under the canopy of *Artemisia* could have increased the total plant growth and canopy cover of some plant species, whereas its allelopathic compounds may have deleterious effects on other plant species. Therefore, lower species diversity under the *Artemisia* can be due to its discriminating effects on the presence of different plant species (Jankju 2013; Motard *et al.* 2011).

CONCLUSIONS

Findings of this research give us some hints on the mechanisms determining vegetation composition of the mountainous rangelands. Accordingly, abiotic environmental parameters (drought and slope aspect) may be more effective on species diversity, whereas the biotic parameter (canopy facilitation) can have greater effects on the total abundance of the mountainous rangelands. While drought and canopy effects are the prominent factors for most growth forms, geophytes species (those reproducing by rhizome, bulb or tuber) may be more responsive to slope aspect, but annuals to drought. Shrubs with larger canopy size, and positive impacts on the soil fertility, may significantly increase species diversity and abundance, and preserve their understory plants against severe drought. However, allelopathic and cushion-like shrubs, may have less impact on species diversity and abundance, because their nursing capabilities can be compromised by their allelochemical compounds and competition for light respectively.

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Conflict of interest statement. None declared.

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