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RESEARCH ARTICLE

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Effects of livestock grazing on plant species diversity vary along a climatic gradient in northeastern Iran

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Abstract

Questions: (a) Do patterns of species diversity and composition differ between plots exposed to high vs. low grazing intensity? (b) Do these differences vary among three regions with different climates, representing a gradient from arid to sub-humid conditions?

Location: Northeastern Iran.

Methods: We compared plots intensively grazed by sheep and goat (HG) to plots with low grazing intensity (LG), across three climatic regions: arid, semi-arid and sub-humid. Species diversity (expressed as Shannon *H*) was compared using linear mixed-effect models. Dissimilarity analysis was used to estimate the compositional heterogeneity of different types of plots, reflecting the differences in species composition. Indicator Species Analysis was used to identify individual species associated with particular types of plots.

Results: The HG plots had lower values of Shannon *H* than LG plots, across all climatic regions. Further, the effect of grazing on species diversity varied between the climatic regions, with the most pronounced differences between the HG and LG plots in the sub-humid region. Although no differences in species diversity were detected between the three climatic regions, compositional heterogeneity was the highest in the sub-humid region and the lowest in the semi-arid region, with the most pronounced differences between the HG and LG plots in the sub-humid region. Indicator Species Analysis showed significant main effects of both climate and grazing on species composition, revealing species that respond to grazing in each of the three climatic regions.

Conclusions: Overgrazing was detected to reduce the diversity of species in all three climatic regions, even though its effect was most pronounced in the sub-humid region. Therefore, the control of overgrazing or reduction of its intensity appears an effective management tool for protecting species diversity, applicable in areas with different climates.

KEYWORDS

climate, diversity, grazing, land use, mountain rangelands, species composition

1 | INTRODUCTION

Predicting and understanding the response of vegetation to environmental and land-use changes have become a major concern in recent ecological research (McIntyre & Hobbs, 1999). In most grassland systems, precipitation (Adler & Levine, 2007) and grazing (Herrero-Jáuregui & Oesterheld, 2018; Zhang et al., 2018) are the most important factors, determining species diversity and ecosystem functioning.

Understanding the effects of precipitation on species diversity is crucial for predicting the impacts of grazing on vegetation, especially in arid and semi-arid climatic regions, where water is the main limiting resource (Yan et al., 2015). The reduced vegetation cover and lower plant diversity increase the susceptibility of rangelands to the effects of climate change (Belgacem & Louhaichi, 2013; Hudson et al., 2014). The effect of climatic changes is often accentuated by shallow soils with low nutrient levels, which limit plant growth and cover and increase the potential for erosion (Hudson et al., 2014).

Disturbance, caused by the overgrazing by large herbivores, is considered as the main cause of land degradation in arid and semi-arid regions worldwide (Zhang et al., 2018). Overgrazing is defined as a decrease of productivity (Adeel et al., 2005) and loss of biodiversity (Sala et al., 2000; Hanke et al., 2014). Intensive grazing directly shifts the composition of plant communities in a selective way, changing the structure and composition of communities at the expense of palatable species (see also Metera et al., 2010; Wan et al., 2015) and may reduce competition by changing the light availability (Rook et al., 2004). Indirect effects of grazing on vegetation include soil compaction through trampling. By trampling, the grazing animals alter the structure and processes in the soil as well, mainly by reducing the soil porosity (Lunt et al., 2007). The damage to the soil structure and the expansion of open surfaces may increase the erosion and deflation of soil (Lu et al., 2017). Overgrazing can also affect the organic matter content of the soil by affecting the processes of mineralization and decomposition (Zhou et al., 2017). Of course, all of these changes affect the species composition.

The impact of high grazing intensity on plant diversity varies along the precipitation gradient (Schultz et al., 2011). In general, the effects of overgrazing on plant species composition and diversity are well documented for most of the world (Dianati Tilaki et al., 2010; Moradi et al., 2016; Wang & Wesche, 2016; Herrero-Jáuregui & Oesterheld, 2018). Rahmanian et al. (2019) focused on the effect of overgrazing on functional diversity of the community and functional traits of individual species present in intensively grazed and minimally grazed plots located in arid, semi-arid and sub-humid climate. Overgrazing was found to affect functional diversity more than climate, even though climate affected soil parameters more than overgrazing. Various studies have found that species diversity declines with an increase of grazing intensity in different regions (Todd, 2006; Hanke et al., 2014), including northeastern Iran (Hassani et al., 2008). In contrast, other studies found no negative effect on diversity attributable to intensive grazing (Todd & Hoffman, 2009; Hanke et al., 2014) or have even detected a positive effect of high grazing intensity on diversity (Wilsey & Polley, 2003; Collins & Calabrese, 2012). The different responses of vegetation to herbivory were mainly explained by the variability in resource availability and grazing history (Milchunas et al., 1988; Lezama et al., 2014), as a high supply of water and nutrients may compensate for the loss of biomass due to overgrazing (Borer et al., 2014). In water-limited environments, intensive grazing is expected to increase plant mortality and therefore decrease species diversity (Ganjurjav et al., 2015). However, recent studies of arid ecosystems have demonstrated that the impact of overgrazing in arid rangelands may be exaggerated and confounded with the effects of climatic change (Sullivan & Rohde, 2002; Zhu et al., 2017). On the other hand, many studies (see for example Proulx & Mazumder, 1998; Herrero-Jáuregui & Oesterheld, 2018) have proposed that species diversity increases with high grazing pressure across a humidity gradient, because of high competition between species in exclosures, particularly in humid environments, where competition for light is intensive. And when the dominant species are grazed, other species have a better chance to survive. The combined effect of climate and grazing on species diversity can be either smaller (antagonistic interaction) or larger (synergistic interaction), than the sum of their individual main effects (De Chazal & Rounsevell, 2009; Ferger et al., 2017). Thus, it is questionable if vegetation responds to overgrazing in a simple, predictable way, making it possible to estimate the future composition of grazed communities in response to climatic change. Therefore, analysis of these potentially interacting factors is crucial to understand the response of biodiversity to overgrazing in the context of a rainfall gradient (Brook et al., 2008; Mantyka-pringle et al., 2012).

According to the United Nations Development Program report, Iran is facing serious environmental challenges. The environmental and natural resources have been substantially degraded, mainly due to unsustainable development and consumption patterns, overpopulation, institutional fragmentation and a number of socioeconomic problems, including social, economic, political, and cultural factors, resulting in the destruction of habitats and ecosystems (United Nations Development Program, 2006). Additionally, these impacts have been amplified by harsh environmental conditions such as frequent and prolonged drought (Madani et al., 2016). Arid and semi-arid rangelands of Iran and the Middle East in general have experienced a long history (>4,000 years) of intensive livestock grazing (Jankju, 2016). The effects of drought and overgrazing have been more intense during recent decades, mostly due to human population growth.

Most results of previous research were based on local studies. Surprisingly, only a few of them were conducted in Iran (Akhani et al., 2013; Mahdavi et al., 2013), especially in its northeastern part (Jafari et al., 2015). The study region offers a unique opportunity to investigate the effects of different grazing levels under distinct climatic conditions. By comparing the effects of grazing on vegetation under contrasting climates, our study contributes to an important issue in the context of the current literature on grazing (but see for example Díaz et al., 2007; Wang et al., 2017). We studied the responses of different plant communities to grazing and aimed to answer the following questions: (a) Do the patterns in species diversity and composition differ between plots exposed to high versus low grazing intensity? (b) Do effects of grazing vary among three regions with different climate, representing a gradient from arid to sub-humid conditions?

2 | METHODS

2.1 | Study region

We selected three different regions, characterized by arid, semi-arid and sub-humid climatic regimes in northeastern Iran in the Khorassan-Kopet Dagh floristic province of the Irano-Turanian region (see Figure 1 and Appendix S1 for more details).

Khajeh Kalat (the driest region in our study system) is located in the eastern Kopet Dagh and classified as a subtropical semi-savanna (Karimi et al., 2009). The area has a dry climate (based on the de Martonne aridity index). The mean annual precipitation (20-year mean) is 255 mm. Most of the flora consists of ephemerals and/or short life-span perennial grasses and forbs. The dominant species is *Pistacia vera*, accompanied by *Artemisia kopetdaghensis*, *Poa bulbosa*, *Amygdalus spinosissima*, *Bunium persicum*, *Ephedra foliata*, *Zygophyllum atriplicoides* etc. (Ahani et al., 2013).

Baharkish rangeland is a semi-arid region in the eastern part of Khorassan-Kopet Dagh. The mean annual precipitation (20-year mean) is 354.4 mm. The main vegetation type is *Artemisia* steppe in mid elevations, thorn-cushion communities with *Acantholimon erinaceum*, *Acantholimon raddeanum*, *Acanthophyllum glandulosum* and *Onobrychis cornuta*, mixed with grasses of mountain steppes (*Festuca valesiaca* and *Stipa* sp.) and also with dwarf shrubs (*Ephedra intermedia*, *Hymenocrater* sp. div. and *Rosa* sp. div.; Memariani et al., 2016a).

Darkesh area represents the sub-humid zone, which is the wettest region within our study system. It is located in the western part of Khorassan-Kopet Dagh. The mean annual precipitation (20-year mean) is 600 mm. Because of topographic and climatic variations, several vegetation types have developed in the area: dense stands of *Juniperus polycarpos* and *Quercus castaneifolia* woodlands in high mountains, *Acer monspessulanum* subsp. *turcomanicum* and *Crataegus* sp. in open shrublands, early successional scrubs with *Paliurus spina-christi* in the foothills, and *Festuca valesiaca* and *Stipa* steppes — sometimes combined with other vegetation types such as grassy montane steppes (Memariani et al., 2016b).

2.2 | Sampling design

The sampling areas were hierarchically arranged in a nested sampling design, with four hierarchical levels: three climatic regions; 6–7 sampling areas in each climatic region; one intensively grazed and one ungrazed site in each sampling area; and 5 HG and 5 LG plots in each of these sites. The size of the studied regions under each climate was 1,600 ha, 1,035 ha and 2,000 ha for the arid, semi-arid and sub-humid conditions, respectively. The sampling areas were of similar size (3–5 ha) across all three climatic regions. The mean distance between individual sampling areas within each of the three climatic regions was 1.63 (±0.51) km and the minimal distance between two sampling areas was 1 km. The HG plots were exposed to heavy grazing (therefore considered as overgrazed and termed "high-grazing plots"; 3 AUM per ha, 90% sheep and 10% goats – see Appendix S3), whereas the LG plots were located within exclosures (and termed "low-grazing plots"). These had been prevented from grazing for around 35 years in all three regions,

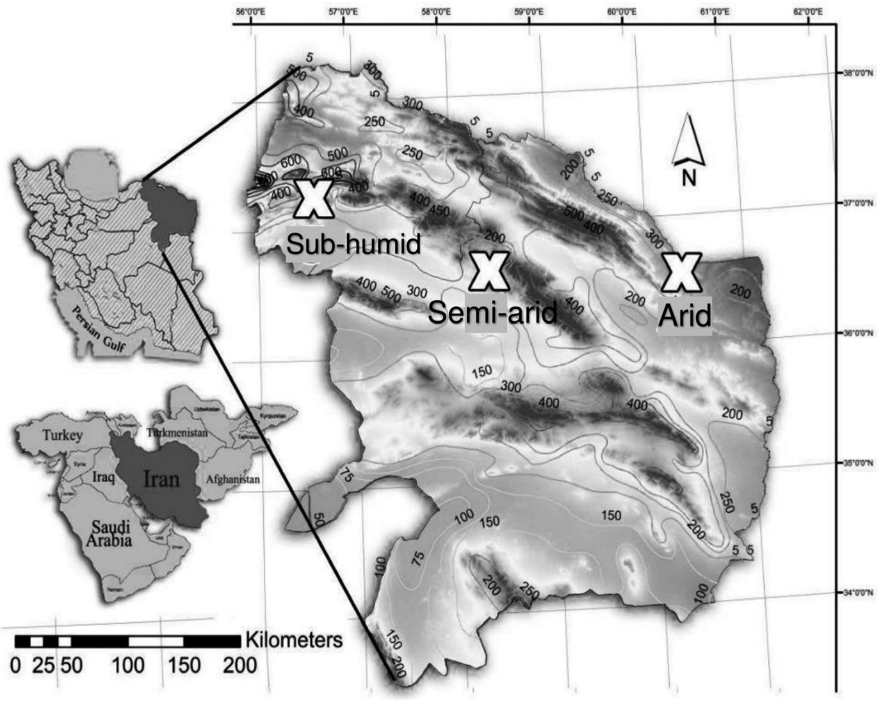

FIGURE 1 Map of the study area in NE Iran, showing the Khajeh Kalat as an arid region, with ~255 mm of annual precipitation, Baharkish rangeland as a semi-arid region, with ~354 mm of annual precipitation, and Darkesh as a sub-humid region, with ~600 mm of annual precipitation (see Appendix S1 for more details on the sampling areas). The fitted surfaces indicate mean annual precipitation

even though occassional grazing by goats has been observed (0.5 AUM per ha), as goats can climb the fences and it is difficult to keep them away (for more information on the grazing history, see Appendix S3). In addition to the grazing status given by the history of the exclosure, we also measured grazing intensity as the median number of droppings (56 ± 12 in the HG and 12 ± 6 in the LG plots) and also as the width of horizontal paths of livestock (0.27 ± 0.09 m for the HG plots and 0.04 ± 0.04 m for the LG plots). Within each sampling area, the mean distance between the LG and HG plots was 20 m. The individual HG/LG plots of 1 m × 1 m were placed randomly, in a relatively homogeneous area in terms of topography, land use and vegetation. This sampling scheme certainly does not include the whole species pool of these habitats. However, our aim was not to describe either flora or vegetation of these regions, but rather to perform unbiased comparisons between the HG and LG analogues (see the species–area curves in Appendix S4). Each plot was characterized by its geographic coordinates and altitude. In 2017, the abundance (cover percentage) of all plant species was recorded between April and June, when the growing season peaks in these regions. The species names were standardized according to Flora Iranica.

2.3 | Statistical analyses

2.3.1 | The effects on species diversity

The differences in species diversity between the HG and LG plots and across the three climatic regions were tested using linear mixed-effect models, with “sampling areas” as random effect (nested in “climatic region”), “climatic region” and “grazing” as fixed effects and Shannon diversity (H) as a response variable. The main effect of grazing was tested in a separate model, in which both the "climatic region" and "sampling areas" were set as random factors, hierarchically arranged. The significance of the individual terms (climate, grazing and climate:grazing interaction) was tested by comparing the models with and without a particular term or interaction. The comparisons were made usig the Aikaike Information Criterion, which evaluates the explanatory power and complexity of individual models (see for example Lukacs et al., 2007). All univariate analyses were performed in the "nlme" package of the R software (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). 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.

2.3.2 | Analysis of the effects on species composition

We estimated the compositional heterogeneity within and between different subsets of the data using the Bray–Curtis distances (ANOSIM package in the "R" software, version 3.5.1; R Core Team, 2018) and tested the differences between different subsets of the data (arid, semi-arid and sub-humid climatic region, LG versus HG plots) using the Dissimilarity analysis framework (Clarke, 1993; R Core Team, R Foundation for Statistical Computing, Vienna, Austria). This analysis is based on comparisons of the ranks of inter-class distances to the ranks of intra-class distances. Then, we separated the compositional heterogeneity among the different subsets of data, defined by climate, grazing and their interaction (permutational multivariate analysis of variance, ADONIS package, R Core Team, 2018).

The fact that the "sampling areas" were nested in "climatic regions" and that the individual plots were nested in the "sampling areas", was treated by the "strata" parameter, which made sure that the plots were permuted within the corresponding levels of the factors above in the hierarchy of the data.

The main effect of grazing was tested in a model where the HG–LG plots were permuted within the sampling areas. This arrangement made sure that the HG–LG plots were permuted within homogenous units, filtering out the spatial effects given by the position of individual sampling areas. Further, we compared the compositional heterogeneity between the HG and LG plots within each climatic region (Table 2). The interaction between climate and grazing was tested in a similar model, with the HG–LG plots permuted within the sampling areas. We used permutation tests (999 permutations — Permutational Analysis of Multivariate Variance: Anderson, 2017) to test the significance of the differences between climatic regions, between the HG vs. LG plots as well as that of the interaction of these two factors. The functions ADONIS and ANOSIM are both part of the "VEGAN" package of the R software (R Core Team, R Foundation for Statistical Computing, Vienna, Austria).

Further, we used Indicator Species Analysis to reveal the preferences of individual species for the HG vs. LG plots, for each climatic region seperately. Using this approach, we can identify species sensitive to grazing. Indicator Species Analysis has two main components: (a) recorded on either HG or LG plots only (exclusivity); (b) recorded on all samples within a particular group (fidelity). We assigned an Indicator Value Index to all species, identifying species with the highest association values. We used permutation tests (999 permutations) 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 Core Team, 2018).

3 | RESULTS

3.1 | Plant species diversity across different grazing intensities and climatic regions

In total, 337 plant species were recorded in all three climatic regions, with 192 species recorded in the sub-humid, 115 in the semi-arid and 137 species in the arid region. No significant differences in mean values of Shannon index (H) of species diversity were detected among the three climatic regions (Table 1). However, the HG plots had lower species diversity (expressed as Shannon *H*), compared to the LG plots across the three climatic regions (Figure 2a). Further, the climate × grazing interaction was statistically significant and the differences between the HG and LG plots were most pronounced in the sub-humid climatic region (Table 1, Figure 2a).

3.2 | Species composition across different grazing intensities and climatic regions

As shown by the tests based on the Bray–Curtis distances (PERMANOVA), the compositional heterogeneity differed significantly between the climatic regions ($p = 0.001$), as well as between the HG–LG plots ($p = 0.001$). The climate × grazing interaction was also significant ($p = 0.001$; Table 2). The effect of grazing was most pronounced in the sub-humid region (Table 2). The ANOSIM also shows that there are differences in the variability explained by the individual terms within the model: the factor climatic region explains more variability in the data ($p < 0.001$; Figure 2b) than the factor grazing ($p = 0.001$; Figure 2b) and their interaction grazing × climatic region (arid: $p = 0.01$, semi-arid: $p = 0.57$, sub-humid: $p = 0.001$; Figure 2b — see Table 2). Moreover, comparison of the explanatory power of the terms within the Dissimilarity analysis shows that the overall effect of the climate × grazing interaction was not larger than the sum of the individual main effects of climate or grazing.

3.3 | Indicator species of different levels of grazing intensity

As shown by the Indicator Species Analysis, *Poa bulbosa*, *Salsola dendroides*, *Avena sterilis*, *Convolvulus arvensis*, *Polygonum arenastrum*, *Verbascum cheiranthifolium* and *Aegilops triuncialis* were more likely to be found on the HG plots, and *Vicia peregrina*, *Cymbolaena grifity*, *Allium rubellum*, *Thalictrum sultanabadense*, *Bromus kopetdagensis*, *Astragalus jolderensis*, *Dactylis glomerata*, *Crupina vulgaris*, *Viola odorata*, *Tanacetum parthenium*, *Vicia sativa*, *Galium tricornutum*, *Quercus castaneifolia* and *Lonicera nummulariifolia* were typical for the LG plots in all three climatic regions (see Table 3 for details and indicator species specific for particular climatic regions).

TABLE 1 Results of linear mixed-effect models testing the effects of climate, grazing and the climate × grazing interaction on species diversity (Shannon *H*)

	DF term	*t*-value	*p*-value
Climate	2	1.277	0.48
Grazing	1	86.978	<0.001***
Climate × Grazing	2	31.275	<0.001***

Note: The main effect of grazing was tested in a separate model, in which “climatic regions” were included among the random effects.
***$p < 0.001$

4 | DISCUSSION

4.1 | Effects of grazing and climate on species diversity

We detected a negative effect of overgrazing on species diversity under the three different climates, that is, across the whole study system (see also Osem et al., 2002; Erfanzadeh et al., 2015; Herrero-Jáuregui & Oesterheld, 2018). The significant effect of grazing on species diversity across different climatic regions in northeastern Iran contradicts the results obtained by a number of field studies from southern African drylands, which found that grazing has little effect on species diversity (Todd & Hoffman, 2009; Rutherford & Powrie, 2013; Saayman et al., 2016). In a series of fence-line studies, Rutherford and Powrie (2010) reported that intense grazing may even increase species diversity of the grazed communities by increasing evenness. Rutherford et al. (2012) reported an increase in evenness due to the suppression of dominant species that resulted in higher species diversity of heavily grazed communities. However, in our study, the high grazing intensity decreased the species diversity, most likely by eliminating the palatable species. This means that the effect of grazing depends on the type of grazed community even within a single climatic situation and, most importantly, it depends on the intensity of grazing (Tóth et al., 2018). In our study, it is therefore likely that the detected suppressive effect of grazing is due to its high intensity, as overgrazing is known to strongly suppress species diversity. Overgrazing is known to cause a non-random, directional loss of species, as the most palatable species are lost first from the community (see also Milton et al., 1994). In addition to species loss, intensive grazing reduces the above-ground biomass. This is partly because the remaining species cannot fully compensate for the species loss due to grazing (Verón et al., 2011) and also due to the defoliation of even the remaining, grazing-tolerant plants. Furthermore, grazing early in the season represents a serious problem for the Iranian and Middle Eastern rangelands. On the HG sites, grazing starts about one month before the major forage plants have grown up enough to protect the soil, which then gets heavily trampled (Ajorlo, 2005; Haji-Rahimi & Ghaderzadah, 2008). Even though extreme arid conditions are known to suppress diversity (Arroyo et al., 1988), we did not detect any significant differences in species diversity between the three climatic regions (see also Ricklefs et al., 2004; Herrero-Jáuregui & Oesterheld, 2018). This may be due to the fact that the precipitation gradient within our study system does not really include extremely dry conditions, in which the species diversity would be limited by drought stress. Most importantly, even though there are no significant differences in species diversity between the climatic regions, we found a highly significant interaction between the effect of climate and grazing on species diversity, with the most pronounced differences between the HG and LG plots detected in the sub-humid region, representing the wettest area in our study system. Apparently, the suppressive effect of grazing was strongest in the sub-humid conditions, where the diversity is unlikely to be limited by drought. This may be partly

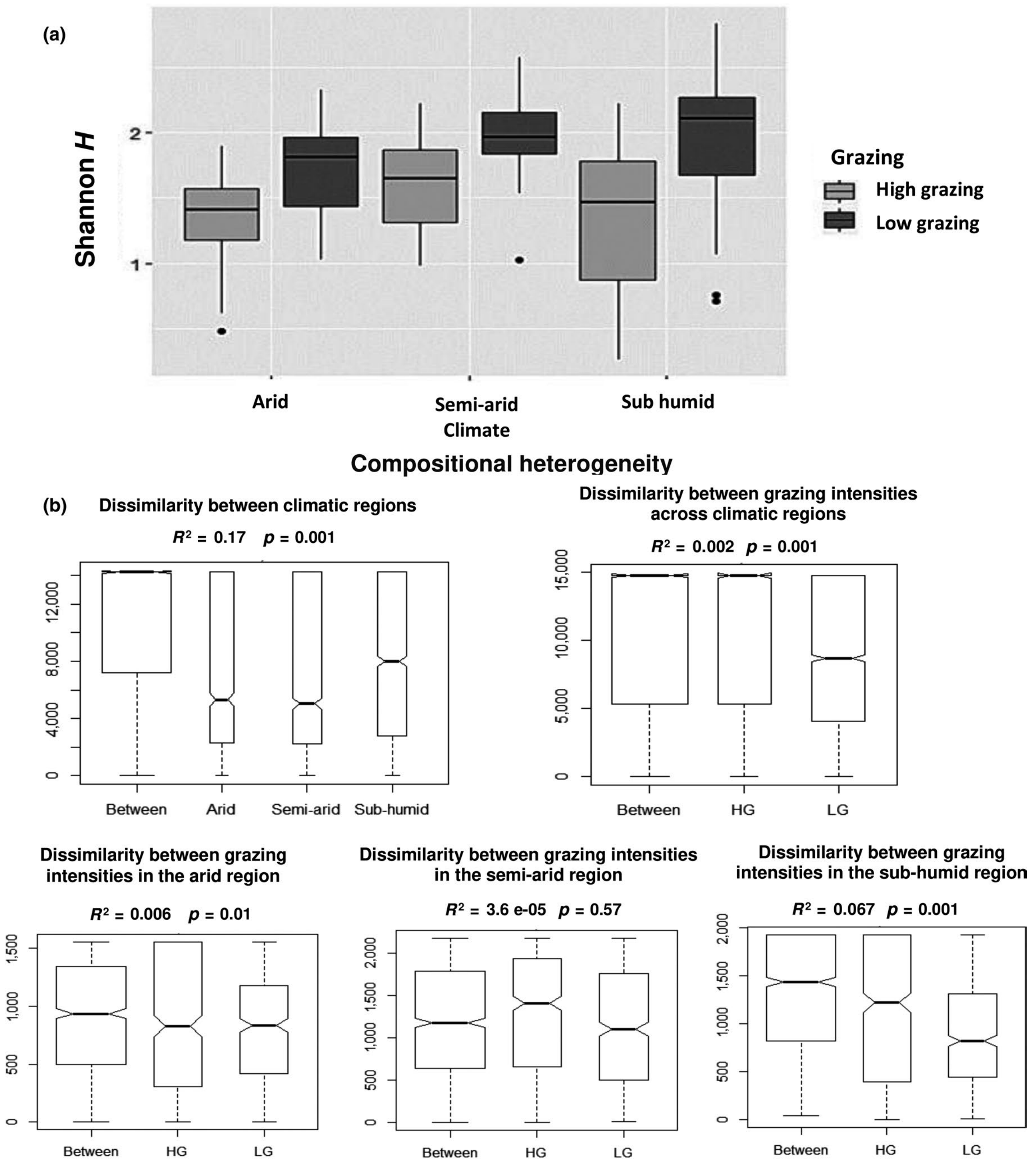

FIGURE 2 (a) Shannon *H* on the high (HG) and low (LG) grazing intensity plots and in the three climatic regions. (b) Using permutation tests, analysis of the dissimilarities provides a way how to test the differences between the climatic regions, between grazing regimes as well as the interaction of these factors. The *y*-axis represents the compositional heterogeneity of different types of plots, expressed by the Bray–Curtis distances. If the groups of sampling units differ in their species composition, then the compositional heterogeneity between groups is larger than that within the groups (999 permutations). The figure shows there are significant differences between the three climatic regions. The differences between the HG and LG intensities are significant in the arid and sub-humid climatic region

due to the high proportion of endemics in this region, which mostly rank among well-palatable species. Further, it is possible that grazing represents the most important limiting factor in conditions that are rich in resources and, therefore, most species are adapted to competition, rather than to the stress and disturbances induced by intensive grazing and trampling (see also Stevens et al., 2012; Lezama & Paruelo, 2016). Given that sub-humid regions receive stable and sufficient precipitation, plant–herbivore interactions may be the main driver of vegetation dynamics (see also Lauenroth & Burke, 2008; Milchunas et al., 2008). In accordance with the non-equilibrium theory (a more dynamic and less predictable perception of ecosystem dynamics accounting for disturbances, spatial heterogeneity, and multiple stable states; Briske et al., 2017), steppes in the arid and semi-arid regions of northeastern Iran differ in their flora and vegetation from the sub-humid region, where most species are adapted to drought and herbivory stress by possessing toxic

TABLE 2 Effects of climate and grazing on plant species composition, based on PERMANOVA (permutation tests with Bray–Curtis distances as importance values and with 999 permutations)

	PERMANOVA	*DF* term	*F*	R^2	*p*-value
Between three climatic regions	Climate	2	10.28	0.09	0.001***
	Grazing	1	3.59	0.01	0.001***
	Climate:Grazing	2	2.92	0.02	0.001***
Within each climatic region	Grazing in the arid region	1	2.74	0.04	0.002**
	Grazing in the semi-arid region	1	1.7	0.02	0.003**
	Grazing in the sub-humid region	1	4.99	0.06	0.001***

***$p < 0.001$

compounds or spiny leaves and stems. Therefore, the differences between the HG and LG plots are less pronounced in the arid and semi-arid region (Rahmanian et al., 2019).

Interestingly, the decrease in species diversity resulting from overgrazing is not necessarily associated with a decrease in the community functional diversity. However, the effect of overgrazing on species diversity ad functional diversity as well as on the representation of individual functional traits was consistently detected to be the most profound in the subhumid climatic region (Rahmanian et al., 2019).

4.2 | Effects of grazing and climate on species composition

Our results confirm the importance of the precipitation gradient in structuring plant communities in northeastern Iran. The heterogeneity in species composition differs significantly between the climatic regions, as well as between the HG and LG plots. The compositional heterogeneity between the HG and LG plots was detected to be largest in the sub-humid region, which is in accordance with the results on species diversity. However, when species diversity decreased due to intensive grazing, compositional heterogeneity increased. This increase may result from the suppression of some species, possibly dominants, by heavy grazing. In a relatively affluent environment, where species can be presumed to be adapted to competition rather than to the stress of aridity, intensive grazing causes massive changes in species composition.

The effect of overgrazing on heterogeneity in species composition is in accordance with the results of Asner et al. (2004), who observed that the increased spatial heterogeneity of vegetation may be an overarching pattern in desertification processes across ecosystems. Intensive grazing may also increase the variation in community composition by promoting the vegetation's patchiness and heterogeneity in resource distribution (de Bello et al., 2007). Spatial heterogeneity can also arise from localized urine and dung deposition, trampling paths, and erosion rills (Olff & Ritchie, 1998). Further, comparison of the explanatory power of the terms within the Dissimilarity analysis shows that the overall effect of the climate × grazing interaction was not larger than the sum of their individual main effects, suggesting that these two factors interact in antagonistically. Species diversity alone does not adequately reflect shifts in vegetation structure in response to intensive grazing in the northeast of Iran. Our results suggest that it is important to consider shifts in species composition as well to achieve a more complex assessment.

The Indicator Species Analysis revealed species typical for each of the three regions, defined by the climate and precipitation (see also Milchunas et al., 1988; Díaz et al., 2007). The significant main effect of grazing is more interesting compared to the main effect of climate (de Bello et al., 2005), as it suggests that there are species sensitive to grazing that are shared by the three climatic regions,. *Quercus castaneifolia* and *Lonicera nummulariifolia* were identified as indicator species of the LG plots, probably because their seedlings and saplings are consumed by grazing animals and can only survive in exclosures. The canopy of these woody species may create a suitable habitat for some herbaceous species, like *Dactylis glomerata*, *Crupina vulgaris* or *Galium tricornutum*. On the other hand, sun flecks and open spaces, caused by the severe grazing, provide an opportunity for ruderal species to establish. Of course, populations of palatable species decline rapidly in grazed habitats (Díaz et al., 2007), being replaced by weedy or ruderal plants (Bullock et al., 2001; Pakeman, 2004), like *Poa bulbosa*, *Aegilops triuncialis* and *Avena sterilis*. These species produce less biomass and are not very attractive for livestock, but compete successfully with other species in the area. Some of the indicator species of the HG plots prefer open areas, such as *Convolvulus arvensis* and *Polygonum arenastrum*. They can germinate and establish better on microsites with bare ground, usually during the early successional stages or after trampling by livestock.

The significant interaction of the effects of climate and grazing shows that specific species respond to grazing in each of the three climatic regions. In the arid and semi-arid regions, the species with a opportunistic strategy, like *Poa bulbosa* and *Galium humifusum*, were only found in the HG plots and palatabale species, like *Vicia sativa* and *Astragalus jolderensisi*, were only found in the LG plots. In the sub-humid region, most species may be competitive rather than tolerant to stress and disturbance and are therefore likely to disappear from the HG plots. This may be the reason that grazing has the most

TABLE 3 List of indicator species for the high (HG) and low (LG) grazing intensity plots in all three climatic regions (arid, semi-arid and sub-humid)

	Arid (A)	Arid (B)	Semi-arid (A)	Semi-arid (B)	Sub-humid (A)	Sub-humid (B)
HG						
Poa bulbosa	0.866**	0.567			0.950*	0.229
Salsola dendroides	0.876*	0.300				
Galium humifusum			1.0000*	0.1714		
Avena sterilis					0.900*	0.257
Verbascum cheiranthifolium					1.000**	0.257
Callicephalus nitens					1.000**	0.229
Convolvulus arvensis					1.000*	0.200
Polygonum arenastrum					1.000*	0.171
Aegilops triuncialis					0.942*	0.171
LG						
Vicia peregrina	0.929**	0.300				
Cymbolaena grifity	0.919**	0.300				
Allium rubellum	1.000**	0.267				
Ferula oopoda	1.000*	0.200				
Thalictrum sultanabadense	1.000*	0.200				
Vicia sativa	0.961*	0.168				
Alyssum singarense			1.000*	0.171		
Bromus kopetdagensis			1.000*	0.143		
Astragalus jolderensis			0.914*	0.229		
Dactylis glomerata					0.881***	0.686
Crupina vulgaris					0.951**	0.286
Galium tricornutum					0.919**	0.286
Quercus castaneifolia					1.000**	0.257
Galium humifusum					1.000**	0.229
Viola odorata					1.000**	0.229
Bromus sterilis					1.000**	0.200
Lonicera nummulariifolia					1.000*	0.200
Acer monspessulanum					1.000*	0.171
Galium spurium					1.000*	0.171
Tanacetum parthenium					1.000*	0.171
Bromus danthoniae					0.974*	0.171
Prunus pseudoprostrata					1.000*	0.143

Note: "A" represents the exclusivity of species, while "B" represents their fidelity. Significances refer to indicator values (A × B) (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; permutations = 999).

profound effect on species composition in the sub-humid region. It was mostly palatable species that were identified as significant indicators of the LG plots in the sub-humid region, such as *Dactylis glomerata*, *Crupina vulgaris*, *Viola odorata* or *Tanacetum parthenium* (see Table 3). Unpalatable species, like *Verbascum cheiranthifolium*, were exlusively found on the HG plots.

Protecting at least some parts of rangelands from overgrazing should help maintain high levels of biodiversity, as well as prevent future economic losses. Most discussions on rangeland degradation have focused on the effects of overgrazing (Eswaran et al., 2001; Asner et al., 2004; Steinfeld et al., 2006). The sustainable management of pastoral ecosystems should seek to find a balance between production and protection of diversity. Such an approach also gives the best chances for sustainable pastoral agriculture.

5 | CONCLUSION

Overgrazing reduces the diversity of species in all three climatic regions. However, the supressive effect of overgrazing on species diversity is most pronounced in the sub-humid climatic region, which is the wettest in our study system. The compositional heterogeneity, expressed by the Bray–Curtis distances, shows a somewhat similar pattern: the differences between the HG and LG plots are most pronounced in the sub-humid region, showing that the reduction of diversity is associated with changes in species composition.

The effect of livestock overgrazing and its interaction with climate was found to be an important factor, limiting the diversity of plants in the rangelands of northeastern Iran. The fact that the negative effect of grazing was detected across the three climatic regions shows that overgrazing is a major, universal problem. These results can be useful for the management of montane rangelands, in the context of global climatic and land-use change.

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AUTHOR CONTRIBUTIONS

HE and MF conceived of the research idea; SR collected data; SR and MH performed statistical analyses; SR with contributions from MH wrote the paper; all authors discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

Data used in this study are given in Appendix S5.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. List of climatic regions

Appendix S2. Scheme of the sampling design

Appendix S3. General description of grazing history in the arid, semi-arid and sub-humid climatic region in northeastern Iran

Appendix S4. The species–area relations of the grazed and ungrazed plots in each of the three climatic regions

Appendix S5. Species composition data

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