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Effects of livestock grazing on soil seed banks vary between regions with different climates

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A R T I C L E I N F O

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A B S T R A C T

The influence of grazing on soil seed bank (SSB) characteristics determines the management of rangelands in different climates. Here we studied the responses of SSBs to livestock grazing in three regions with different climates – arid, semiarid and subhumid – in northern Iran. In each region 30 pairwise SSB samples were collected on 1 m^2 plots, 15 in intensely grazed areas and 15 in ungrazed areas. The total SSB densities, their diversity and species richness and the densities of functional groups were compared between the grazed and ungrazed plots and between the climatic regions. Both climate and grazing as well as their interaction affected SSB characteristics. Although the results of the non-metric multidimensional scaling (NMDS) showed noticeable differences in SSB species composition between grazed and ungrazed plots in all three regions, the magnitude of the grazing effect on the SSB was different between climatic regions. In total, 119 species germinated from the soil samples: 33 species in semiarid, 39 species in arid and 61 species in subhumid samples. The highest total SSB density, diversity (Shannon index) and richness were found in subhumid climate with an average of 138.90 seeds/m^2, $H = 2.27$ and 17.83 species/sample, respectively. In ungrazed areas the average SSB density was 26.60 seeds/m^2, 46.06 seeds/m^2 and 195.90 seeds/m^2 in arid, semiarid and subhumid climate, respectively. In grazed areas the corresponding figures were 12.40 seeds/m^2, 7.00 seeds/m^2 and 110.40 seeds/m^2. Averages of SSB diversity in ungrazed areas were 1.24, 1.60 and 2.42 in arid, semiarid and subhumid climates, respectively, as compared to 1.27, 0.97 and 2.20 in grazed areas. The averages SSB richness in ungrazed areas were 5.21 species/sample, 7.54 species/sample and 21.25 species/sample in arid, semiarid and subhumid climate, respectively, whereas in grazed areas 4.00 species/sample, 2.86 species/sample and 16.15 species/sample were found on average. Overall, intensive grazing was linked to lower SSB characteristics in all three climatic regions, but the size of the effect differed between the climatic regions. Thus, we concluded that the impact of grazing on SSB density, diversity and richness is climate-dependent. Hence, the climatic conditions have to be considered when evaluating the effects of grazing on soil seed banks.

1. Introduction

The soil seed bank (SSB) is an important part of plant communities, and its studies can provide important information for restoration and management (Yusefi et al., 2021). The SSB determines essential ecological processes in maintaining biodiversity (Lee and Marrs, 2021) and might support the recovery of degraded plant communities (Mohammed and Denboba, 2020). SSBs can be a major propagule source, which can have a significant effect on vegetation composition and diversity (Rusvai and Czóbel, 2021). Seed banks are also essential in

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processes related to the resilience of plant communities (Yang et al., 2021). Nevertheless, the spatial and temporal variation of SSBs, their sizes and composition changes caused by disturbances in different climates are not fully understood (Erfanzadah et al., 2022).

It is well known that livestock grazing is an important driver for the composition and structure of aboveground vegetation (Lezama et al., 2014). Through the consumption of plant biomass and trampling, livestock grazing can promote strong changes in vegetation composition and production of grasslands worldwide (Nakano et al., 2020; Silva and Overbeck, 2020). However, several studies showed that the magnitude of grazing effects on vegetation in different ecosystems depends on environmental conditions such as soil and climate (e.g., Török et al., 2016; Rahmanian et al., 2019). For example, a more pronounced effect of grazing on plant community composition and thus an increasing dissimilarity between grazed and ungrazed sites was observed in grasslands with increasing soil fertility and productivity (Osem et al., 2004). In productive habitats high grazing intensity led to areas usually dominated by clonal plants (Johansen et al., 2016) and maximum plant diversity (Zanella et al., 2021). In addition, the intermediate disturbance hypothesis indicated that in productive habitats the highest plant diversities were observed at moderate disturbance levels (Hobbs and Huenneke, 1992), whereas in unproductive areas similar patterns were less pronounced. Tahmasebi Kohyani et al., (2008) observed greater differences in plant community composition between grazed and ungrazed plots in nutrient-rich sites compared to sites with a lower nutrient availability, and Martin et al. (2022) found significant effects of soil and grazing interaction on vegetation characteristics. In addition, Rahmanian et al. (2019) demonstrated that the effects of livestock grazing on standing vegetation vary between regions with different climates. Thus, the responses of aboveground vegetation to livestock grazing under different environmental conditions have been continuously studied and are relatively well known, whereas comparative studies of grazing effects on the belowground vegetation (e.g. effects on soil seed banks) in different environments are scarce. However, information on the density and composition of the SSB under grazing is important to better understand the potential of vegetation recovery in degraded sites after overgrazing. SSB studies in grazed grasslands can thus contribute to the planning of ecological restoration (see e.g. Buisson et al., 2018). However, most SSB studies around the world are limited to a comparison between grazed and ungrazed areas in a single climate or region (e.g. Erfanzadeh et al., 2016). Whereas studies on the effects of grazing on the SSB during a year showed that these effects were different depending on the seasonal climatic conditions (Chu et al., 2019), only very few studies evaluated the effects of grazing on the SSB characteristics in different climates. We therefore aimed to test whether livestock grazing in different climatic regions has a similar effect on the SSB. We assumed that the magnitude of the effect of grazing on the SSB is climate-dependent so that changes in the SSB characteristics due to grazing are different in different climatic regions.

Precisely, as some plants increase their vegetative growth as an alternative form of reproduction under grazing and therefore contribute less to the seed bank (Erfanzadeh et al., 2020) and intensive grazing can reduce seed production through the consumption of palatable (and sometimes unpalatable) species before they set seed and consequently deplete soil seed bank potential (Erfanzadeh et al., 2016), we hypothesised that i) the SSB density and diversity decrease with grazing intensity. In addition, since humidity may promote seed production, it can be supposed that ii) the SSB density is higher in more humid climate. Moreover, in dryer habitats the seed bank of plants, particularly annuals, is exposed on the soil surface throughout the year, and germination takes place at the soil/air interface easily after any sporadic rain (Mott, 1974), depleting the SSB density and diversity. Therefore, iii) the soil seed bank is shaped by both grazing and climate, and the magnitude of SSB decrease via grazing is higher in humid than in arid regions.

2. Material and methods

2.1. Study area and sampling

We selected three regions with different climates in northern Iran for sampling: two regions with semiarid and subhumid climate in the Mazandaran province and one region with arid climate in the Golestan province (Table 1). In all three regions there are sharp gradients of livestock grazing, ranging from very intensive to ungrazed, all within small and therefore relatively homogeneous areas. The climatic conditions are very heterogeneous, with a mean annual rainfall varying from less than 300 mm in the arid region to more than 750 mm in the subhumid region. Sheep are predominantly used for grazing in all three regions, with a stocking density of approx. 5 adult sheep per ha. The sheep breeds kept in the Mazandaran and Golestan province are Zel and Dalagh, respectively. Although different types of grazing animals may differ in their effects on vegetation (Tóth et al., 2018), a quite similar impact on plant communities has been validated for different breeds of sheep, which are all capable of picking individual plants or plant parts such as flowers, pods and young shoots with their incisors (see also Oliván and Osoro, 1998). In each region grazing animals had been excluded from small areas for at least 20 years prior to the field work (in 2021) to study plant succession after removal of grazing (Fig. 1). The Iranian Research Institute of Forests and Rangelands supported the exclosure trials in order to provide experimental evidence for their habitat management strategies for the areas. Therefore, the exclosures were constructed within grazed areas in places where the vegetation was representative of the entire area to assess aboveground vegetation and SSB changes after grazing removal in each climate (see also Marco and Páez, 2000). The three selected regions were i) Pasperes (subhumid climate with an average annual temperature and rainfall of 15.5 °C and 751 mm, respectively, and a monthly average temperature ranging from 0.8 °C in January to 30.2 °C in July), ii) Kiasar (semiarid climate with an average annual temperature and rainfall of 12.0 °C and 600 mm, respectively) and iii) Chaparghoymeh (arid climate with an average annual temperature and rainfall of 17.1 °C and 291 mm, respectively, and a mean total rainfall of 27.5 mm from November to May).

2.2. Vegetation and soil sampling

In each region one sampling site of 600 m × 600 m was selected in both grazed and ungrazed areas. The sampling sites were located to be representative of the entire habitat in that location (Heady and Child, 1994). Within each sampling site 15 plots of 2 m × 2 m were randomly placed. Soil samples were collected in March 2021, when the natural stratification of seeds had already taken place in the field (van Tooren, 1988). With an auger of 5 cm diameter, 10 soil cores were randomly collected to a depth of 5 cm in each plot and combined. In total 30 soil samples were collected in each region: 15 samples from the grazed and 15 from the ungrazed area. The vegetation composition was assessed during the growing season of 2022 on the plots that had been used for the soil sampling in the year before. The cover of each vascular plant species was visually estimated using a percentage scale (Londo, 1976).

In addition, 3–4 soil cores were randomly collected from each plot and combined for chemical analyses. Organic matter was determined by the loss of ignition method (Lal et al., 2001), and total soil N was assessed by wet oxidation using the Kjeldahl method (Zagal et al., 2009). Soil pH and electrical conductivity (EC) were assessed in soil–water suspension in the ratio of 1:2.5 (weight/volume). Soil pH was measured using a glass-electrode pH meter, EC by using a conductivity meter (Zandi et al., 2017).

2.3. Greenhouse germination

Following Chen et al. (2022), propagule parts such as buds and bulbils were not removed from the soil samples. The soil samples were

Table 1
Climatic and edaphic characteristics in the three sampled regions in the provinces of Golestan (Chaparghoymeh region) and Mazadaran (Kiasar and Pasperes regions).

Region	Climate	Coordinates	Elevation (m)	Mean annual precipitation (mm)	Soil pH	Soil EC (Ms/cm)	Soil organic matter (%)
Chaparghoymeh	arid	37° 25′ 57″ N 55° 05′ 33″ E	80	291	8.80	282.71	1.71
Kiasar	semiarid	36° 14′ 19″ N 53° 46′ 39″ E	1600	600	8.38	126.58	1.63
Pasperes	subhumid	36° 22′ 88″ N 51° 14′ 75″ E	1740	750	7.32	250.00	2.58

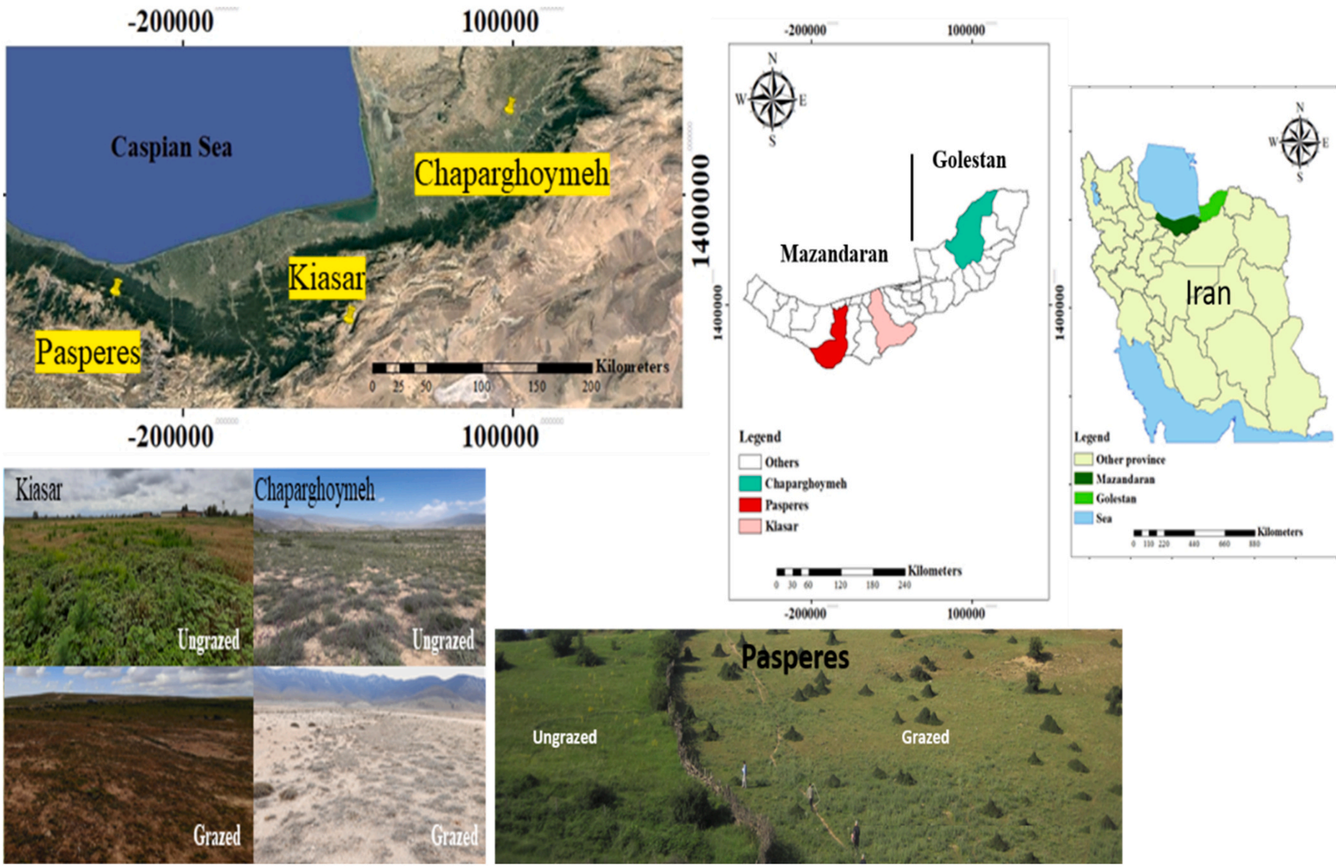

Fig. 1. Geographic location of the study regions Chaparghoymeh, Kiasar and Pasperes in two adjacent provinces (Mazandaran and Golestan) in Northern Iran.

spread in a thin layer of maximum 4 mm thickness in 40 cm × 40 cm trays onto a 4 cm layer of a sand and sterilised potting soil mixture. The trays were placed randomly on shelves in a greenhouse with a natural light regime and kept moist by regular watering. Air temperature varied between 14 °C and 25 °C during the germination. Fifteen control trays filled with a mixture of sand and sterilised soil were also placed randomly on the shelves to test for possible greenhouse and air-borne contamination.

Seedlings were identified as soon as possible after germination, counted, and then removed. Seedlings that could not be identified immediately were transplanted to pots to allow further growth until identification. Plant species nomenclature follows Rechinger (1964).

After 25 weeks, when no further seedlings emerged, the trays were left to dry for two weeks. This allowed the samples to crumble, thus exposing deeper buried seeds to the light. Watering was then reinitiated and continued for another two weeks, but no new seedlings emerged. Finally, the soil was checked for remaining seeds by examining small random samples under a microscope and by probing seeds with a needle in order to distinguish between firm and empty seeds.

2.4. Statistical analyses

Firstly, we carried out a non-metric dimensional scaling (NMDS) to visually analyse the distribution of soil seed bank composition in the space delimited by data disturbing (6 groups: three regions and two grazing intensities) (Kottler and Gedan, 2020). To make the data comparable, we used relative frequencies for NMDS analysis by dividing the total SSB density of each species in a given sample by the total SSB density of all species in that sample. The NMDS analysis was carried out using R version 4.3.1 (R Core Team.. 2023) and the 'vegan' package (Oksanen et al., 2019).

Total SSB density, species richness and the density of each functional group (annuals (grasses + forbs), perennials (grasses + forbs), forbs (annuals + perennials), grasses (annuals + perennials) and shrubs and Raunkiær's life-form scheme (Ellenberg and Mueller-Dombois, 1967)) in the SSB were calculated, as well as the Shannon diversity index (*H*) according to Magurran (2004).

The data were checked for homogeneity of variance and normality using Levene's test and the Kolmogorov-Smirnov test, respectively. Two-way ANOVA was used to compare SSB characteristics between different regions and between grazed and ungrazed areas. The regions (nominal) and the presence of grazing (binary) were included as fixed factors, the SSB characteristics as dependent variables. Since the interaction between region and grazing was significant in most cases, we also used unpaired *t*-tests to compare SSB characteristics between grazed and ungrazed areas in each region. All statistical analyses were carried out using SPSS 17.0 (SPSS Inc, USA; www.spss.com).

3. Results

3.1. Species composition in the soil seed bank and aboveground vegetation

In total, 119 species germinated from the soil samples: 33, 39 and 61 species from Kiasar, Chaparghoymeh and Pasperes samples, respectively. The dominant plant species in the SSB were *Stipa hohenackeriana*, *Phalaris tuberosa* and *Poa pratensis* in Kiasar, Chaparghoymeh and Pasperes, respectively (Table S1). In Kiasar the dominant plant species in the SSB were *Agropyron repens* in grazed and *Stipa hohenackeriana* in ungrazed plots. In Chaparghoymeh the dominant plant species in the SSB were *Allium cristophii* and *Phalaris tuberosa* in grazed and ungrazed plots, respectively. In Pasperes the dominant plant species in the SSB were *Gastridium phleoides* and *Poa pratensis* in grazed and ungrazed plots, respectively. A detailed list of species with calculated seed densities is given in Table S1.

In the aboveground vegetation 144 species were recorded in total. In Kiasar, Chaparghoymeh and Pasperes, 52, 33 and 80 species were observed, respectively. The dominant plant species were *Artemisia sieberi*, *Lolium temulentum* and *Medicago minima* in Kiasar, Chaparghoymeh and Pasperes, respectively.

The NMDS results showed a separable grouping of SSBs for grazed and ungrazed plots in all three regions (Fig. 2).

3.2. Effect of climate, grazing and their interaction on total density, diversity and richness of the SSB

The effects of region, grazing and climate × grazing interaction on the total SSB density, diversity and richness were all significant (Table 2).

The highest total SSB density, diversity and richness were found in subhumid climate with an average of 138.90 seeds/m^2, $H = 2.27$ and 17.83 species/sample, respectively. The lowest values were observed in the arid region with an average of 19.50 seeds/m^2, $H = 1.25$ and 4.61 species/sample, respectively. The main effect of grazing was significant on SSB characteristics, whose figures were much higher in ungrazed plots (Table 3). The average SSB densities in ungrazed areas were 26.60 seeds/m^2, 46.06 seeds/m^2 and 195.90 seeds/m^2 in arid, semiarid and subhumid climate, respectively, whereas in grazed areas 12.40 seeds/m^2, 7.00 seeds/m^2 and 110.40 seeds/m^2, respectively, were found.

Table 2
Results of general linear models testing the effects of climate, grazing and climate × grazing interaction on soil seed bank characteristics.

Density	Sum of squares	df	Mean square	F	Sig.
Climate	313382.35	2	156691.17	127.23	0.000
Grazing	46214.85	1	46214.85	37.53	0.000
Climate×Grazing	18312.44	2	9156.22	7.44	0.001
Diversity					
Climate	19.97	2	9.98	63.57	0.000
Grazing	1.60	1	1.60	10.18	0.002
Climate×Grazing	1.68	2	0.84	5.36	0.006
Richness					
Climate	3508.48	2	1754.24	263.12	0.000
Grazing	286.02	1	286.02	42.90	0.000
Climate×Grazing	65.74	2	32.87	4.93	0.009

In arid, semiarid and subhumid climate, the average SSB diversity was 1.24, 1.60 and 2.42, respectively, in the ungrazed areas and 1.27, 0.97 and 2.20, respectively, in the grazed areas.

The average SSB richness was 5.21 species/sample, 7.54 species/sample and 21.25 species/sample in arid, semiarid and subhumid climate, respectively, in the ungrazed areas and 4.00 species/sample, 2.86 species/sample and 16.15 species/sample, respectively, in the grazed areas.

In the arid, semiarid and subhumid region, total SSB densities in grazed areas were significantly lower than in ungrazed areas (Table 4 and Table 5). In the semiarid and subhumid region total SSB diversity and richness were lower in grazed than in ungrazed areas, whereas in the arid region no significant differences in total SSB diversity and richness were observed between grazed and ungrazed areas (Table 5).

3.3. Effect of climate, grazing and their interaction on functional groups of the SSB

Soil seed bank densities of different functional groups of plants varied between different climates (Table 4). SSB densities of annuals, forbs and therophytes were highest in the subhumid region, whereas

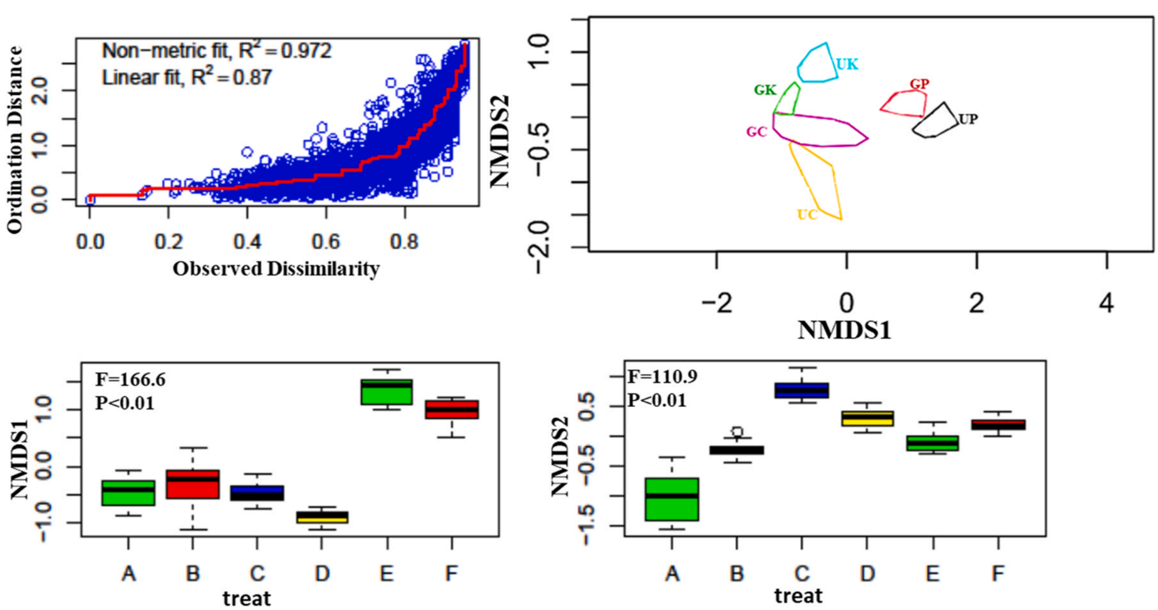

Fig. 2. Non-metric multidimensional scaling (NMDS) of the soil seed bank (SSB) composition in the upper soil layer (0–5 cm) (Stress=0.017). GC: Grazed plots in Chaparghoymeh, UC: ungrazed plots in Chaparghoymeh, GK: grazed plots in Kiasar, UK: ungrazed plots in Kiasar, GP: grazed plots in Pasperes and UP: ungrazed plots in Pasperes.

Table 3
Soil seed bank characteristics (mean values and corresponding standard errors (SE)) recorded on grazed (G) and ungrazed (U) plots in each of the three climatic regions.

		Total density	SE	Shannon diversity	SE	Total richness	SE
Climate (both G and U plots)	Arid	19.50	2.51	1.25	0.07	4.61	0.38
	Semiarid	26.53	4.54	1.28	0.09	5.21	0.55
	Subhumid	138.90	12.71	2.27	0.05	17.83	0.76
Grazing (in all climatic regions)	Grazed	49.98	7.45	1.55	0.09	8.52	0.94
	Ungrazed	76.22	13.47	1.67	0.09	10.07	1.14
G and U plots (within each of the climatic regions)	Arid-G	12.40	1.86	1.27	0.12	4.00	0.47
	Arid-U	26.60	4.01	1.24	0.09	5.21	0.57
	Semiarid-G	7.00	1.15	0.97	0.13	2.86	0.44
	Semiarid-U	46.06	5.62	1.60	0.09	7.54	0.53
	Subhumid-G	110.40	5.80	2.20	0.05	16.15	0.58
	Subhumid-U	195.90	29.61	2.42	0.10	21.25	1.51

Table 4
Soil seed bank density (seeds/m^2, mean values and corresponding standard errors (SE)) of each functional group.

		Main effect of grazing in all three climatic regions				Main effect of climate on both grazed and ungrazed plots					
	Responses	Grazed	SE	Ungrazed	SE	Chaparghoymeh (arid)	SE	Kiasar (semiarid)	SE	Pasperes (subhumid)	SE
Functional groups	Annuals	35.20	12.00	30.08	8.85	14.63	3.79	18.35	6.38	41.64	11.18
	Perennials	8.08	1.99	14.09	3.80	16.26	4.31	26.87	11.14	8.27	2.18
	Forbs	17.50	5.48	17.01	4.42	10.57	2.60	13.30	4.65	18.71	4.34
	Grasses	10.32	2.60	41.11	16.12	25.35	5.58	42.08	15.15	17.78	13.89
	Therophytes	30.98	12.24	25.09	6.71	14.00	3.69	21.37	6.10	34.33	10.77
	Hemicryptophytes	10.21	3.10	23.94	9.04	21.33	6.30	35.57	23.35	15.32	5.57
	Cryptophytes	2.01	1.00	2.12	1.01	2.02	0.57	2.02	1.03	2.01	0.57
	Chamaephytes	3.00	1.22	7.51	1.90	5.40	1.55	6.80	1.65	7.50	1.90
	Geophytes	15.28	8.10	12.58	8.52	13.53	6.90	12.58	8.58	13.60	6.47

Table 5
Results of non-paired *t*-tests comparing soil seed bank characteristics between grazed and ungrazed areas in each region.

Responses	Chaparghoymeh (arid)			Kiasar (semiarid)			Pasperes (subhumid)		
	df	*t*-value	Sig	df	*t*-value	Sig	df	*t*-value	Sig
Total density	28	3.20	0.003	28	6.80	0.00	28	3.84	0.00
Shannon diversity	28	-0.19	0.84	28	3.93	0.00	28	1.93	0.06
Total richness	28	1.61	0.11	28	6.71	0.00	28	3.73	0.00
Annuals	20	1.10	0.20	18	1.81	0.08	72	0.59	0.55
Perennials	13	1.05	0.31	14	0.97	0.34	110	0.41	0.68
Forbs	17	0.10	0.92	17	1.32	0.20	142	0.16	0.86
Grasses	12	2.70	0.01	10	2.44	0.03	26	0.73	0.46
Therophytes	19	0.98	0.16	21	1.97	0.06	66	0.80	0.42
Hemicryptophytes	7	0.46	0.65	5	0.96	0.37	78	0.99	0.32
Chamaephyte	2	0.20	0.86	2	3.02	0.09	-	-	-
Geophyte	2	1.09	0.39	-	-	-	20	0.31	0.75

perennials, grasses and hemicryptophytes had highest SSB densities in the semiarid region. No significant differences between the regions were observed for the other functional groups (Table 4).

In the subhumid region the SSB density of annuals was significantly higher than that of perennials (mean of 41.61 seeds/m^2 vs. 8.27 seeds/m^2), whereas in the semiarid region it was the other way round (mean of 18.35 seeds/m^2 vs. 26.87 seeds/m^2). In the arid region there was no significant difference between the SSB density of annuals and perennials (mean of 14.63 seeds/m^2 and 16.26 seeds/m^2, respectively) (Table 4). In the arid and semiarid region the SSB density of grasses was significantly higher than that of forbs (25.35 seeds/m^2 vs. 10.57 seeds/m^2 and 42.08 seeds/m^2 vs. 13.30, respectively), whereas in the subhumid region there was no significant difference in SSB density between grasses and forbs (Table 4).

Annuals (therophytes) were higher in ungrazed areas than grazed areas in semiarid region ($P<0.1$, marginal significancy) and grasses were higher in ungrazed areas than grazed areas in arid and semiarid regions ($P<0.01$). Grazing had no significant effects on SSB of other functional groups in any climate (Table 5).

4. Discussion

This study indicated that overall, grazing suppressed the SSB consistently across all study areas. This suggests that grazing is a significant factor, limiting soil seed bank density and species diversity across all climatic regions. However, the magnitude in which the soil seed bank responded to grazing were different in different climates; the effect was lowest in the driest and wettest climate and highest in the intermediate climate.

4.1. Main effects of grazing on the SSB

This study showed that high grazing intensity had a significant and destructive effect on the soil seed bank in all studied regions. This effect may result from above-ground vegetation consumption or trampling by livestock. It is generally assumed that grazing reduces cover, height and above-ground biomass in most vegetation types in different regions and climates (Schonbach, 2011). In a meta-analysis of data Shi et al. (2022) showed that heavy grazing had a negative effect on soil seed bank characteristics, particularly on species richness. Grazing can decrease SSB density and richness through decreasing seed production in various plant species (Xie et al., 2016). It has been shown that a variety of seed production metrics (e.g. reproductive shoot number, flower number, fruit number, seed mass and reproductive biomass) decreased through intensive grazing for many plant species (Xie et al., 2016; Ma et al., 2018). It can therefore be assumed that continuous over-grazing may decrease the aboveground plant yield in our study regions as well, both because of intensive biomass consumption and because of destruction of plant roots by trampling livestock (see also Solomon et al., 2006; Erfanzadah et al., 2022). Consequently, the seed production capacity of plants and their ultimate contribution of seeds to the seed bank will be reduced. Sites with cessation of grazing typically possessed a greater number of species and density in the soil seed banks compared to grazed and disturbed sites due to significant effects of grazing on aboveground plant material (Li et al., 2017). In addition, compaction of the soil surface by trampling may inhibit the penetration of seeds into the soil and thus enhance their risk to be consumed by seed predators, resulting in a soil seed bank decrease (Erfanzadah et al., 2022). Moreover, livestock grazing can deplete seeds buried in soil through seed germination facilitating (Liu et al., 2023). It was indicated that disturbance and the creation of canopy gaps facilitated germination from seeds for many short-lived and competitively inferior species (e.g. Milberg, 1993), and grazing animals can create the germination conditions needed by these species by trampling, poaching and opening up the sward (Bakker and Olff, 2003). In addition, grazing can also have indirect negative effects on the SSB by changing soil parameters: Ma et al. (2018) demonstrated that grazing disturbance decreased summer SSB density through its indirect effect on soil moisture and total nitrogen.

Among functional groups the SSB density of chamaephytes and hemicryptophytes decreased strongly by livestock grazing. These species are often assumed to be intolerant to grazing due to the accessibility of their buds (Dupré and Diekmann, 2001), with negative effects of grazing on plant production leading to a decrease in seed input to the soil. However, we found the SSB density of Therophytes (annuals) to be significantly higher in grazed areas. Some studies reported that grazing increased the SSB density and the species richness in the soil seed bank through its effects on annual plants and persistent seeds (Chu et al., 2019). In addition, some species are less grazed by livestock due to their low palatability. Our data showed that many seeds that germinated from samples collected in the grazed plots (particularly in Pasperes) belonged to a few species such as *Veronica persica* and *Gastridium phloides*. These annual species have the capability to produce many seeds (e.g. Bitarafan and Andreasen, 2022), and their secondary metabolites are unpalatable for grazers (e.g. Kim et al., 2020). The combination of these two characteristics gives these species an advantage in heavily grazed areas.

4.2. Main effects of climate on the SSB

The main effect of climate (region) on the soil seed bank was significant in our study. Besides different climates, different ecosystems also have different soil seed banks. The SSBs of woodlands, for example, differ significantly among ecosystem types: Mangroves, tundra and tropical dry broadleaf forests were found to have lower SSB diversities than Mediterranean forests, subtropical moist broadleaf forests and tropical coniferous forests. In these ecosystems the climate is considered to be a major determinant of soil seed bank characteristics (Yang et al., 2021). Climatic factors such as precipitation and temperature have been shown to be strong soil seed bank drivers. Precipitation influences the success of sexual reproduction of plants and the size of the seed bank through seed input (Ooi, 2012). It also affects soil pathogenic fungi (Delavaux et al., 2021), which cause seed mortality (Beckstead et al., 2010). Therefore, precipitation has a strong effect on SSB density, as also reported for 27 alpine meadows on the Tibetan Plateau (An et al., 2020). Yang et al. (2021) illustrated that precipitation in the driest quarter and in the driest month of the year are the key factors determining seed bank density worldwide, suggesting that moisture fluctuation in soils triggered by precipitation in the driest time of the year can affect seed bank density. In addition, SSB density peaked when the temperature of the warmest month was relatively high (Yang et al., 2021). We also believe that the seed inputs in different regions into the soil were different due to the effects of different climatic conditions on standing vegetation characteristics such as seed production by plants. Vegetation type and the responses of cover, height, species richness and plant production at various spatial scales have been shown to be influenced by climatic gradients (e.g., Su et al., 2017). Erfanzadeh et al. (2013) demonstrated that SSB density and diversity varied along an altitudinal gradient due to the effects that different climatic conditions in different altitudes have on aboveground vegetation. Although our literature review showed that the effects of climatic conditions on soil seed banks have scarcely been studied (e.g. Yang et al., 2021), a study on the seasonal variation of SSBs indicated that climatic factors are a robust driver for SSBs due to their effects on vegetation (Shen et al., 2007). Seed input is an important factor in determining the seasonal pattern of soil seed banks. Seeds of plants are dispersed after ripening, and the number of seeds produced by plants is large in the peak of growth, which results in high seed bank densities in the soil (Garcia et al., 2020).

4.3. Effects of grazing and climate interaction on the SSB

Although the results of the NMDS showed that grazed and ungrazed plots could be separated with regard to their SSB species composition in all three regions, the magnitude of the grazing effect on the SSB differed between the regions. The highest negative impact of grazing on the SSB was found in Kiasar, a region with moderate climatic conditions (e.g. precipitation 600 mm vs. 291 mm in Chaparghoymeh and 751 mm in Pasperes). More precisely, grazing decreased the total SSB density by 84% in Kiasar (semiarid climate), but only by 53% in Chaparghoymeh (arid) and by 44% in Pasperes (subhumid). Similar patterns were found for total SSB species richness and SSB diversity (Table 3). We assume that the effects of grazing on the SSB are less pronounced in arid than in humid regions, but further studies involving a sufficient number of study areas in both extreme climates are needed to corroborate this hypothesis.

Previous studies showed that changes in aboveground vegetation by grazing are associated with climatic factors. It was found that with increasing precipitation, the trends in species richness and plant production in the aboveground vegetation of grasslands changed from a linear form in ungrazed areas to a unimodal relationship in grazed areas (Bai et al., 2012). These studies indicated that climatic conditions play an important role in regulating the responses of community structure and ecosystem function to grazing. In some studies, the changes in the aboveground vegetation were reported to be highest under mild climatic conditions. Gamoun (2014) reported that grazing decreased plant species richness under moderate climatic conditions (i.e. meadow steppe and typical steppe), but had no significant effect on species richness under harsh conditions (i.e. desert steppe and desert). These differences in the effects of grazing on standing vegetation in different climates should also be reflected in the soil seed bank.

Besides the indirect impact of grazing on the size of the SSB through vegetation consumption, grazing can also affect the SSB by changing chemical and physical soil parameters, and these effects are related to climatic conditions. It has been reported that the effect of grazing on the physical properties of the soil is influenced by precipitation and temperature (Yan et al., 2008; Gong et al., 2023). For example, when the air temperature increases, the positive effect of grazing on the soil bulk density and soil temperature and the negative effect on soil moisture will become increasingly obvious. When the annual precipitation exceeds 500 mm, the response of soil temperature to grazing becomes less obvious (Yan et al., 2008; Gong et al., 2023). Furthermore, several studies showed that SSB characteristics are associated with soil physical factors (moisture in Pakeman et al., 2012; clay and sand in Nascimento e

Souza et al., 2019; porosity and bulk density in Kamali and Erfanzadeh, 2014; clay and silt in Luo et al., 2021). Since the effects of grazing on physical soil properties are different in different climates, the indirect effects of grazing on soil seed banks should be climate-dependent as well.

5. Conclusion

Our observations indicate that climatic conditions play an important role in regulating the responses of soil seed bank characteristics to grazing. By considering the combined findings of our study in three regions with different climates, we provided evidence that the composition of the soil seed bank differed between grazed and ungrazed grasslands and that the climatic conditions have to be considered when evaluating the effects of grazing on soil seed banks. However, restoration of grasslands under different climates after heavy grazing is possible in any climate in this study, considering climate conditions is advised.

CRediT authorship contribution statement

Razavi Bahar S: Conceptualization, Investigation, Writing – original draft. **Török Péter:** Conceptualization, Formal analysis, Investigation, Validation, Writing – original draft, Writing – review & editing. **Hazhir Shadi:** Data curation, Writing – original draft. **Erfanzadeh Reza:** Conceptualization, Data curation, Formal analysis, Methodology, Supervision, Writing – original draft. **Ghelichnia Hassan:** Data curation, Investigation, Methodology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.108901.

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