Community Ecology (2022) 23:75–85
https://doi.org/10.1007/s42974-021-00074-3

ORIGINAL ARTICLE

The effect of shrub community on understory soil seed bank with and without livestock grazing

Reza Erfanzadah[1] · Fatemeh Barzegaran[1] · Siroos Saber Amoli[2] · Julien Pétillon[3]

Received: 31 October 2021 / Accepted: 15 December 2021 / Published online: 29 January 2022

Abstract
Shrub communities often modify understory soil and vegetation characteristics. However, the effect of individual shrubs on the soil seed bank (y6SSB) could be variable in grasslands depending on the presence of grazing. We examined how grazing influences patch-level effects of shrubs on local soil seed bank (SSB) density, species richness, and composition. Twenty individuals of *Crataegus pseudomelanocarpa* (dominant woody species in the study area) were randomly selected in the degraded ecotone between forest and grassland in northern Iran, 10 in grazed and 10 in ungrazed areas. Soil samples were collected under shrubs and the space between shrubs and then transported to the greenhouse. The seedling emergence method was used to estimate SSB density and composition in the greenhouse. In total, 61 species germinated from the soil samples with 47 species in the grazed sites (43 species in shrub, 34 species in open) and 54 species in the ungrazed sites (43 species in shrub, 46 species in open). SSB density and richness were significantly lower under shrubs compared with outside in the ungrazed areas while the converse results were found in the grazed areas. Although grazing decreased SSB density and species richness, this decrease was less pronounced under the shrubs, indicating the nursing roles of shrubs against grazing on seed production by herbaceous plants.

Keywords *Crataegus pseudomelanocarpa* community · Disturbance · Facilitation · Hyrcanian forests

Introduction

Grasslands play a prominent role in providing ecosystem services for humans. Currently, the degradation of these ecosystems is globally occurring due to human activities and inappropriate management such as intensive livestock grazing (Loydi et al., 2012). Overgrazing is regarded as a dominant factor in causing grassland degradation (Akiyama & Kawamura, 2007) and can threaten the ecological integrity of grasslands and the sustainability of pastoralist societies that depend on these ecosystems for their livelihood (King, 2008). Previous studies have reported that grasslands have been damaged by overgrazing through reductions in vegetation coverage, plant diversity, and biomass deterioration (e.g. Schonbach et al., 2011; Sanou et al., 2018). As a result, overgrazing caused low seeds production and incorporation into the soil (Erfanzadeh et al., 2016) and overall decreased soil seed bank (SSB) density.

The presence of woody plant species could mitigate the effects of overgrazing. Woody plant species could reduce this impact by acting as nurse plants that facilitate the growth and development of other herbaceous species beneath their canopy and induce the autogenic development of soil as "fertile islands" (Ren et al., 2008). Facilitation is known as an important process in the development of the diversity and composition of plant communities (Hupp et al., 2017; Ramirez et al., 2015). It helps to improve and modify environmental conditions under the crown cover, reduce environmental stresses, create appropriate microhabitats and grow of other species (Falster et al., 2018; Howard

✉ Reza Erfanzadah
Rezaerfanzadeh@modares.ac.ir

Siroos Saber Amoli
Saberamolisiroos@gmail.com

Julien Pétillon
julien.petillon@univ-rennes1.fr

[1] Rangeland Management Department, Faculty of Natural Resources, Tarbiat Modares University, Tehran, Iran

[2] Research Division Natural Resources Department, Mazandaran Agriculture and Natural Resources Research and Education Center, AREEO, Sari, Iran

[3] UMR CNRS Écosystèmes, Biodiversité, Evolution, Université de Rennes, Rennes, France

et al., 2012; Hupp et al., 2017). Nurse plants often improve stressful environmental conditions in a way that increases the diversity of species (Pugnaire and Lazaro, 2000; Falster et al., 2018). From a theoretical point of view, one may envisage that the facilitation role of woody plants becomes more important when introducing grazers into the system (Danet et al., 2017). Conversely, it is likely that the relative importance of facilitation decreases in overgrazed areas since unpalatable-protective plants are also being grazed (see also Smit et al., 2007). Although the functions of nurse plants have been studied in different ecosystems around the world, including grasslands (e.g. Cavieres et al., 2006; Soliveres et al., 2015), the effect of this nursing role on SSB has rarely been compared between grazed and ungrazed areas, with few field studies showing that woody species facilitated establishment of other plant species in the grazed areas (e.g. Smit et al., 2007; Gonzales & Ghermandi, 2019). It is well known that plants protect other plants from herbivores in two general ways (Callaway et al., 2000). Benefactors may have anti-herbivore characteristics such as spine or toxics, and other species take advantage of being near heavily defended plants (McAuliffe, 1984). Herbaceous species may also benefit from being hidden in a crowd, or by taking advantage of diverse neighbors that make them more difficult to locate for herbivore (Brown & Ewel, 1987). Therefore, it can be supposed that the role of shrub patches in maintaining SSB was much more pronounced in the grazed compared to the ungrazed areas.

In this study, specifically, we aimed to answer two questions: (1) what is the effect of woody plant communities (here Crataegus *pseudomelanocarpa M.* Pop. ex A. Pojark) (Rosaceae family) on the SSB of temperate grasslands and (2) how does the effect of woody plants on SSB change when associate with overgrazing pressure?

Materials and methods

Description of the study area

This study was carried out in Iran, within the Alborz mountain chain in Vaz watershed (extending between latitudes 51° 52.14′ 75″ N and 51° 52.28′ 90″ N and longitudes 36° 22.29′ 88″ E and 56° 22.38′ 43″ E). Two main domains are recognizable along the altitudinal gradient in Alborz: Temperate-Hyrcanian forest and grasslands. The dominant woody species in the forest habitat is *Fagus Orientalis* (Esmailzadeh et al., 2011) with a rich cover of herbaceous species in the sub-stratum, e.g. *Asperula stellina* and *Brachypodium pinnatum*. The ecotone between forest and grassland is a boundary where shrub and tree species spread into a matrix of herbaceous species, like *Galium* spp. and *Poa pratensis* (see "Appendix"). All three habitats (forest, ecotone, and grassland) have been grazed for many years by sheep (mostly in the grasslands: five sheep per hectare) and cattle (mostly in the forest: the number of cattle per hectare is unknown), creating bare soil gaps due to intensive and continuous grazing in the ecotone and grasslands. Temperature decreases with increasing elevation from the forest to the grassland. The ecotone has the highest plant diversity and richness due to suitable environmental conditions compared with the forest and grassland (Erfanzadeh et al., 2013). The climate is humid subtropical with average annual temperature and rainfall, 15.5 °C and 550 mm, respectively and, a monthly average temperature ranging from 0.8 °C (January) to 30.2 °C (July). The soil type is Brown that formed under favorable climate conditions and is rich in organic matter (Eskandarie, 2012; Khaleghi, 1998).

Site selection and soil sampling

In a small part of the ecotone (ca. 110 ha), grazing animals were excluded in 2006 (from 2004 to 2006, grazing was also excluded in the growing season) for restoration and conservation management. This exclosure created an opportunity to study some vegetation and soil parameters compared to the grazed areas. *Crataegus pseudomelanocarpa* (Mozaffarian, 2007) is the dominant shrub in the ecotone. Twenty individuals of *C. pseudomelanocarpa* (hereafter called a patch) were randomly selected in grazed and ungrazed areas (10 in grazed and 10 in ungrazed areas). The distance between any two sampling patches was at least 100 m. Personal observation showed that domesticated browsing changed the architecture of *C. pseudomelanocarpa*, leading to massive and closed lateral branches in the shrub. However, to determine SSB characteristics, we selected similar shrub individuals in size (2.5–3 m in diameter: very small and very large individuals were ignored in our random selections) in the grazed and ungrazed areas and collected soil samples under the canopy of *C. pseudomelanocarpa* and the interspace between *C. pseudomelanocarpa* individuals (hereafter called interpatch) using a 5 cm-diameter auger to a depth of 10 cm. The sampling surface area in each interpatch was equal to the surface of its pair-patch using plots, 2 m × 3 m (the crown canopy of C. *pseudomelanocarpa*: 5–7 m^2). In each patch, 10 soil cores were collected beneath the canopy and 10 soil cores were collected outside the canopy. Soil sampling was conducted in early autumn 2017, after seed dispersal. Thus, the germinable seeds contained transient and persistent components of the SSB. According to the protocol of Thompson et al. (1997), soil cores were divided into two depths (0–5 cm and 5–10 cm) (Erfanzadeh et al., 2013). The soil cores were combined for each depth and stored at 2–4 °C in darkness for 5 weeks before greenhouse processing (artificial cold stratification) (Miller & Cummins, 2003).

Then, soil samples were transported to the greenhouse for seed germination studies (80 soil samples in total).

Seed germination experiment

Seedling emergence method was used for SSB composition identification (Erfanzadeh, Daneshgar, et al., 2020a, b). Each soil sample was spread over 3 cm thickness of sterilized potting soil and sand (1:1) in free-draining plastic trays of 25 cm × 35 cm, totaling 80 trays (2 depths × (20 patches + 20 interpatches)) in the greenhouse. Eight control trays containing only sterile potting soil and sand were placed at random with the samples to test airborne contamination. All trays were kept under natural light and temperature conditions and moist by artificial watering (Niknam et al., 2017). Germinated seedlings were identified, counted, and removed once they reached an identifiable stage during greenhouse study (30 weeks). Plant species were identified using publications about the flora of Iran (Ghahraman, 1986–2014; Rechinger, 1964; Mozaffarian, 2007).

The plant species of aboveground vegetation (AGV) were listed in each patch and interpatch in both grazed and ungrazed areas during the growing season, June 2018. Estimation of AGV characteristics (e.g. percentage cover of each plant species) was not possible in the patches due to the compact branches of the shrub in the grazed areas. Therefore, the presence of plants under each individual shrub was recorded. However, vegetation sampling was done in the soil sampled plots in the interpatches in both grazed and ungrazed areas.

Statistical analyses

Seed density was calculated for each 5 cm soil depth layer and for each species separately in all samples in grazed and ungrazed areas and in both locations (patch and interpatch). Seed density was recalculated according to the number of seeds per m^2. The number of species in each soil sample was considered as species richness. SSB similarity between the species composition of the AGV and the SSB was assessed with the Jaccard similarity index for all samples (Eq. 1) (Kent & Coker, 1995). We used presence-absence data for both SSB and AGV to calculate the similarity index.

$$SS\% = a/a + b + c \quad (1)$$

In which: SS = Jaccard similarity index, a = number of species in both SSB and AGV, b = number of species in SSB only, and c = number of species in AGV only.

The normal distribution of the results (seed density, species richness, and AGV-SSB similarity) was checked by the Smirnov-Kolmogorov test. Total richness, SSB-AGV similarity, and $\log_{10}$ (total seed density) followed the normal distribution.

To investigate the effect of the patch, depth, grazing (as fixed factors) and their interactions on density and species richness of SSB and AGV-SSB similarity, a three-way ANOVA (general linear model) was used. In addition, t-tests were used to compare SSB characteristics between patches and interpatches, between grazed and ungrazed, and between depths. All statistical analyses were done using SPSS ver. 17.

In addition, to compare the composition and abundance of species in the SSB between patches and interpatches in grazed and ungrazed areas, non-metric multidimensional scaling (NMDS) was performed (Kottler & Gedan, 2019) using the package 'vegan' in R ver. 3.6.1 (Oksanen et al., 2019).

Results

Diversity and community composition in Above-ground vegetation and soil seed bank

In total, 80 and 61 species were found in the vegetation and SSB, respectively. Thirteen species were present in the SSB while absent in the vegetation, and 31 species were present in the vegetation while absent in the SSB ("Appendix").

We recorded 34 species (1320 seedlings) in the interpatches and 43 species (1655 seedlings) under the shrubs (patches) in the grazed area (47 species in total) and, 46 species (2019 seedlings) in the interpatches and 43 species (1100 seedlings) under the patches in the ungrazed areas (54 species in total) ("Appendix"). The most dominant families in the SSB were Fabaceae and Asteraceae with 8 and 6 species, respectively.

Although the main effect of grazing on AGV-SSB similarity was not significant (Table 1), a relatively high AGV-SSB similarity was observed in the upper soil layer in the grazed area (Fig. 1).

The composition of SSB was clearly separated between grazed and ungrazed sites (the NMDS Axis 1, Fig. 2). The composition of SSB was clearly separated between patches and interpatches in the grazed sites (the NMDS Axis 2, Fig. 2). The composition of SSB in the ungrazed area showed no clear separation between patches and interpatches (Fig. 2).

Soil seed bank density and richness variations

All fixed factors had a significant effect on soil seed bank density and richness (Table 1). The SSB density significantly varied between patches and interpatches in the ungrazed areas with the highest number in the interpatches (Fig. 3).

Table 1 The effects of grazing, patch, and depth (fixed factors) and their interactions on soil seed bank density, richness, and similarity between aboveground vegetation and soil seed bank

Source	Log_{10} seed density (seeds per m^2)			Richness			Jaccard similarity index		
	df	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Grazing	1	21.35	0.00**	1	34.32	0.00**	1	1.01	0.32
Patch	1	3.49	0.01*	1	1.82	0.18	1	2.29	0.14
Depth	1	43.99	0.00**	1	73.31	0.00**	1	0.07	0.79
Grazing × Patch	1	14.46	0.00**	1	25.17	0.00**	1	0.20	0.66
Grazing × Depth	1	0.06	0.79	1	0.04	0.83	1	12.36	0.00**
Patch × Depth	1	0.01	9.38	1	0.47	0.49	1	6.87	0.01*
Grazing × Patch × Depth	1	0.76	0.38	1	0.15	0.69	1	1.52	0.22

**Significant at $p < 0.01$; *significant at $p < 0.05$

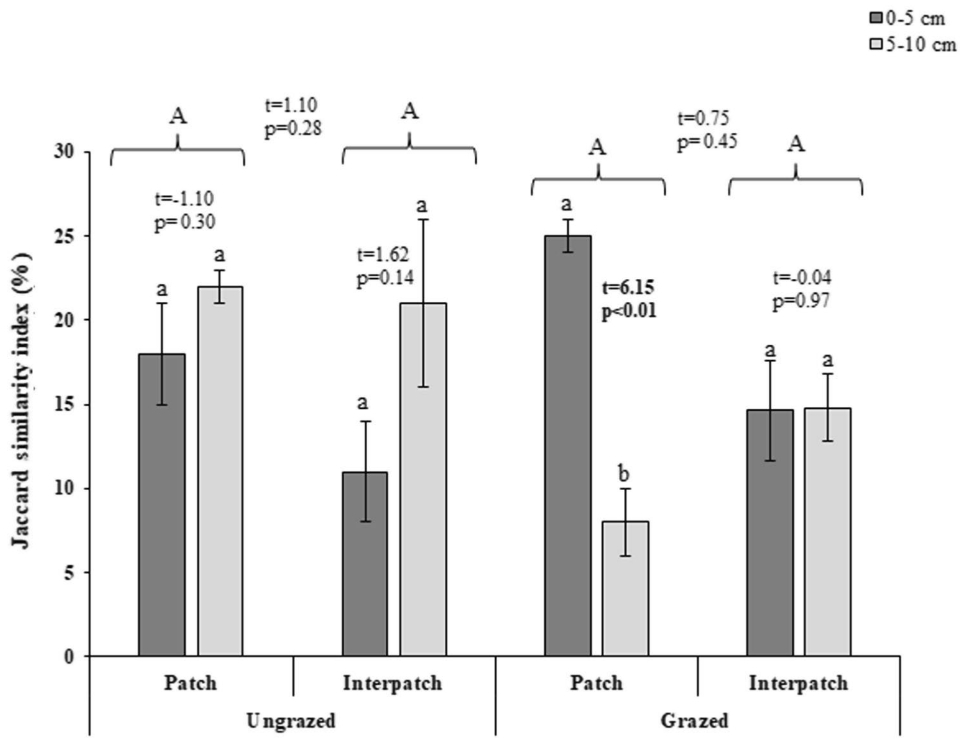

Fig. 1 Average of Jaccard similarity index between soil seed bank and aboveground vegetation (± SE) in the deferent locations beneath and outside the patches in grazed and ungrazed areas. Small successive letters indicate significant differences between two depths in each patch (or interpatch) and capital successive letters indicate significant differences between patches and interpatches in grazed (or ungrazed) areas. Results with significant differences are shown in bold format

The highest seed number was found in the upper soil layers (Fig. 3). In addition, comparing grazed with ungrazed areas, the highest seed number was found in the ungrazed areas (Table 1). SSB densities were similar between patch and interpatch in the grazed area (Fig. 3).

Species richness of SSB was significantly higher in the ungrazed areas compared with grazed areas (Table 1, Fig. 4l). In the ungrazed areas the highest number of species was found in the interpatches while in the grazed areas, the highest number of species was found in the patches (Fig. 4). Generally, SSB richness was higher in the upper soil layer compared with the deeper soil layer (Fig. 4).

Discussion

Similarity between aboveground vegetation and soil seed bank

Low similarity between AGV and the SSB in our study area (8–25%) was in accordance with some previous studies (e.g. Erfanzadeh et al., 2014; Tessema et al., 2017) and in contrast with others (e.g. Plue et al., 2021). Many species were recorded in the aboveground vegetation while absent from SSB and vice versa. In addition, some species were perennial, and are well known for their transient seed bank due to the asexual reproduction (Erfanzadeh et al., 2016). Some

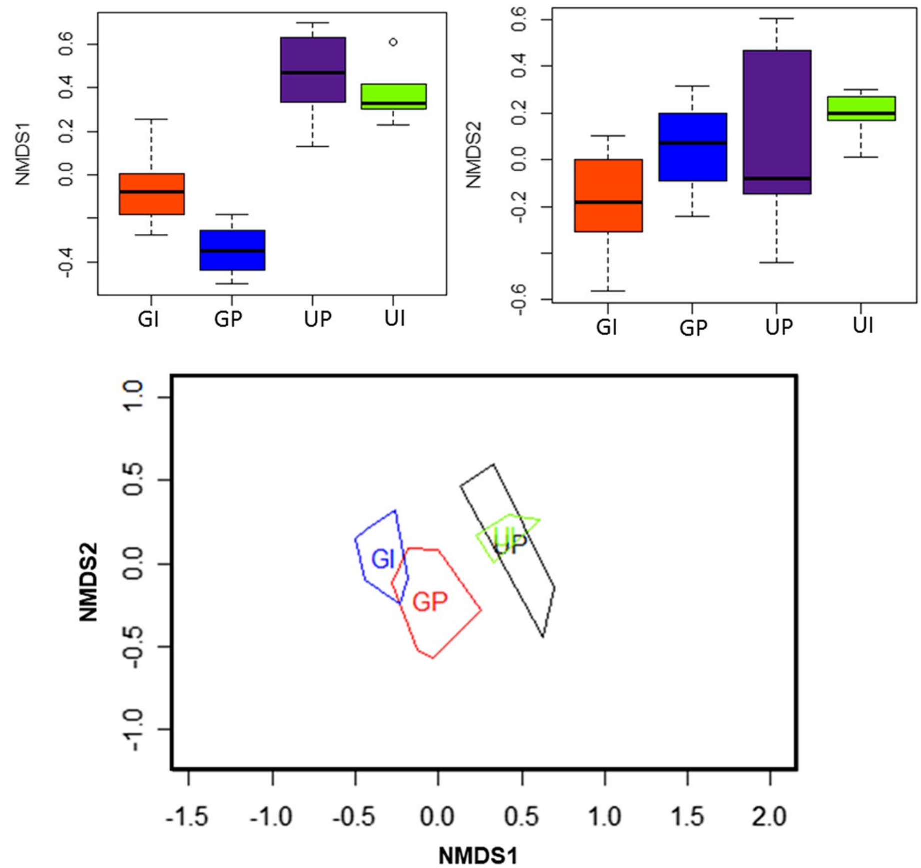

Fig. 2 Non-metric multidimensional scaling (NMDS) of soil seed bank (SSB) composition between four locations including GI (interpatches in the grazing area), GP (patches in the grazing area), UI (interpatches in the ungrazing areas), and UP (patches in the ungrazing areas) ($R2 = 0.96$ for Non-metric fit, $R2 = 0.79$ for Linear fit and Stress = 0.03)

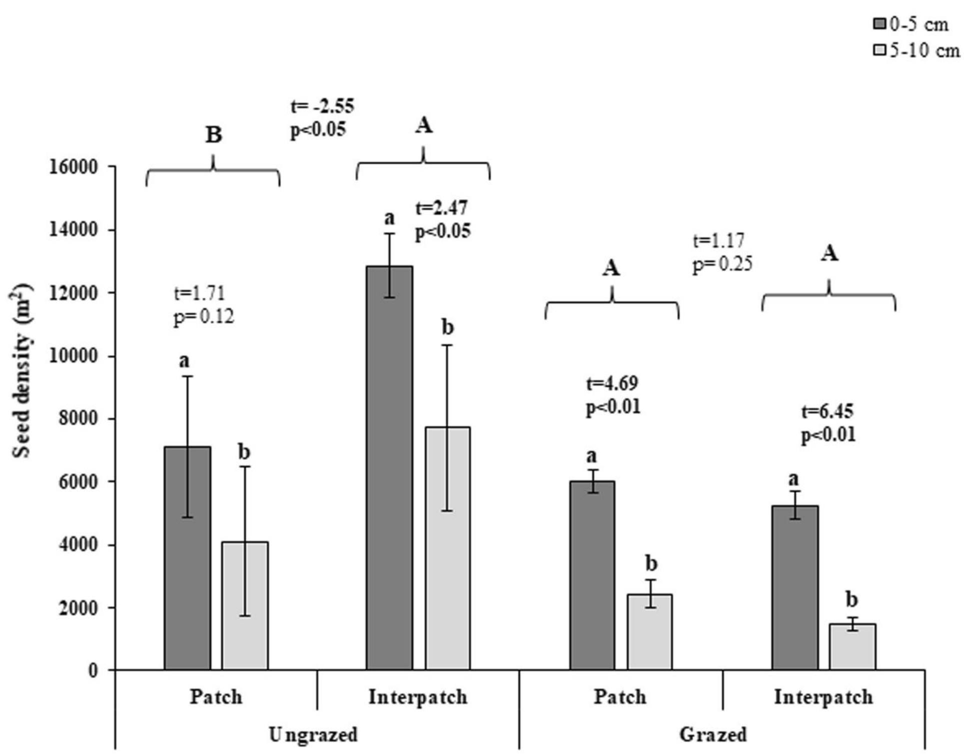

Fig. 3 Average of soil seed bank density (± SE) beneath and outside the patches in grazed and ungrazed areas. Small successive letters indicate significant differences between two depths in each patch (or interpatch) and capital successive letters indicate significant differences between patches and interpatches in grazed (or ungrazed) areas. Results with significant differences are shown in bold format

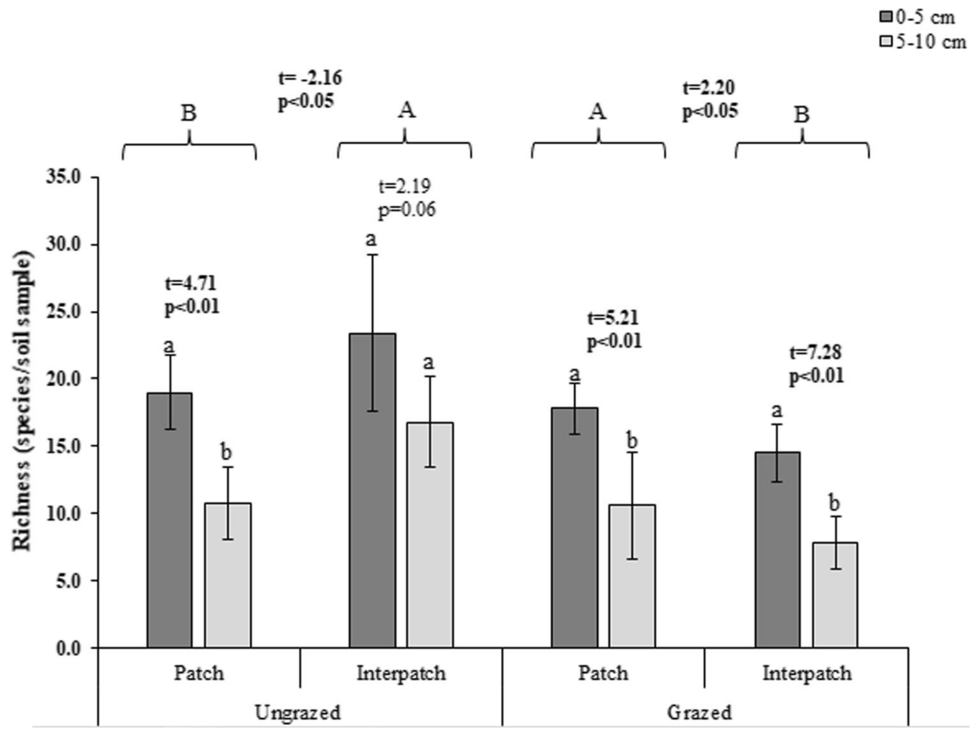

Fig. 4 Average of soil seed bank richness (± SE) in the deferent locations beneath and outside the patches in grazed and ungrazed areas. Small successive letters indicate significant differences between two depths in each patch (or interpatch) and capital successive letters indicate significant differences between patches and interpatches in grazed (or ungrazed) areas. Results with significant differences are shown in bold format

perennials such as *Dactylis glomerata* are clonal which probably increased their vegetative growth as strong competitors and therefore contributed less to the seed banks. However, the highest similarity between SSB and AGV was recorded in the grazed area under the shrub canopy in the upper soil layer. In the grazed area, many species, such as *Poa nemoralis*, *Taraxacum serotinum,* and *Viola odorata* were common between SSB of the upper layer and AGV that indicated the facilitative role of shrubs in seed production of herbaceous species under their canopies in grazed areas.

Ordination by NMDS showed that the species composition of the SSBs in the grazed area was very different from the SSBs in the ungrazed area. These differences emerged due to two reasons: (1) total seed bank density (non-significant) and richness (significant) were lower in the grazed than ungrazed areas; (2) Many species were found in the SSB of ungrazed areas while they were absent in the grazed area, e.g. *Bromus sterilis* and *Cardaria draba*. These species are mostly are being grazed particularly in the vegetative growth stage. Adversely, many species of the SSB were found in the grazed areas while they were absent in the ungrazed area, e.g. *Dianthus Orientalis* and *Lycopus europaeus*. Probably seeds of unpalatable and non-attractive species to animals (e.g. *D. Orientalis* and *L. europaeus*) led to higher seed production and emerged in the SSB in the grazed area. Unpalatable species tend to have higher SSB density in the grazed areas compared with the ungrazed areas (Erfanzadeh, Daneshgar, et al., 2020a, b).

Effect of grazing and shrub (patch) on soil seed bank characteristics

The results of this study showed that livestock grazing, in total, decreased SSB density and species richness. Ungrazed and undisturbed sites typically possess a greater number of species and density in the seed banks compared to grazed and disturbed sites (Li et al., 2017). 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 with increasing grazing intensity for many plant species (Xie et al., 2016). Therefore, it can be deduced that with continuous over-grazing, the aboveground plant yield can be decreased, both because of heavy utilization and destruction of plant roots by trampling livestock (also Solomon et al., 2006). Consequently, the production capacity of plants and their ultimate contribution of seeds to the seed bank is reduced. In addition, compaction of the soil surface by trampling may inhibit the penetration of seeds into the soil and consume by seed predators before penetrating.

The effect of shrubs on SSB density and richness was positive in our grazing areas. In accordance with previous studies (Erfanzadeh et al., 2014; Giladi et al., 2013; Tessema et al., 2017), our results showed a relatively higher seed number and richness buried in soil under the shrubs when compared with outside. Generally, woody patches accumulate large and diverse SSBs beneath their canopies, which consequently enhances seed density and richness in soil. This accumulation is due to a very high amount of seed input by seed trapping and, producing by herbaceous plant species within patches (Braz et al., 2014; Filazzola et al., 2019). Seeds transported by wind and water are trapped in soil surface beneath shrubby patches and penetrate into the soil. In addition, more suitable conditions beneath the shrub canopies versus animal grazing, facilitate growing and colonization of herbaceous, which eventually increases seed production by herbaceous species and finally increases SSB density and species richness under the shrub canopies.

However, in the ungrazed areas, the patches showed a negative effect on SSB density and richness in our study. Differences in the shrub architectures may create these different spatial variations of SSB density and richness between grazed and ungrazed areas. The mature ungrazed shrubs of *C. pseudomelanocarpa* grow with a vertical-upright single stem. Naturally, the canopy structure is open unattached to the ground. While in the grazed areas, the shrub canopy showed a procumbent denser structure. This dense structure might increase the nursing role of shrub against grazing for seed production and their roles in trapping seeds.

Effect of depth on soil seed bank characteristics

Soil seed number and species richness showed a decreasing trend with depth, both being significantly higher in the upper layers than in the lower layers (for all patches and interpatches in both grazed and ungrazed areas). Many other studies have reported similar trends of decreasing seed density with increasing soil depth (e.g. Erfanzadeh et al., 2014; Hu et al., 2019; Ma et al., 2010; Menezes et al., 2019). Although many factors, including seed size and shape, affect seed persistence and the depth that seeds are able to penetrate (Thompson 2000), the majority of viable seeds are normally concentrated in the first few centimeters of the soil surface (Erfanzadeh et al., 2016) since they have been reached to the soil surface recently. In addition, similar to water-logged soils, some plants might reduce survival of seed in deeper depths due to a lower amount or lack of oxygen or light (Saatkamp et al., 2014).

Finally, seeds of shrubs and trees were not abundant in the SSBs in our study. It is well known that seeds of woody species are not abundant in temperate areas because they are not able to produce a persistent SSB and generally have a transient or short-lived seed bank (Esmailzadeh et al., 2011; Thompson, 2000). Lack of a persistent seed bank explains why woody species were not represented in the seed bank. Nevertheless, we found seeds of *C. pseudomelanocarpa* in ungrazed areas while not present in the grazed areas. Livestock grazing on twigs was probably an effective factor that influenced seed production by woody species.

Conclusions

Although grazing decreased soil seed bank density and species richness, this decrease might be less pronounced under the shrubs due to nursing roles of shrubs on seed production and trapping. Therefore, from the point of view of restoration, our findings provide useful guidelines for identifying potential facilitators in degraded, intensively grazed grasslands in which shrubs that are resistant to grazing in an ecosystem are likely candidates for being uses in restoration. Indeed, woody species in intensively grazed grasslands can help the ecosystem to conserve plant diversity through SSB and should be considered for restoration and maintenance.

Appendix: Average soil seed bank density (per m^2) of each species beneath (patch) and outside (interpatch) of *Crataegus pseudomelanocarpa* crown cover in grazed and ungrazed areas

Species	Family	Ungrazed area				Grazed area			
		Patch		Interpatch		Patch		Interpatch	
		0–5	5–10	0–5	5–10	0–5	5–10	0–5	5–10
Achillea millefolium L.	Asteraceae	10.18*	0*	142.66*	10.18*	0	0	5.09*	0*
Aethionema sp.	Brassicaceae	0	0	0	10.18	0	0	0	0
Allium sp.	Alliaceae	591.02	101.9	438.17	10.18	427.98	183.42	132.47	66.23
Anagallis arvensis L.	Primulaceae	0	0	0	0	0*	0*	0	0
Arabis sagittata (Bertol.) DC	Brassicaceae	0*	0*	0	0	0	0	0	0
Arenaria leptoclados (Rchb.) Guss	Caryophllaceae	10.18	0	50.95	20.38	163.04*	25.47*	0*	5.09*
Artemisia annua L.	Asteraceae	1110.7	2027.8	2078.76	3250.6	305.7*	397.41*	351.55*	585.92*
Arnebia sp.	Boraginaceae	0	0	0*	0*	0	5.09	0	0
Bromus racemosus L.	Poaceae	0*	0*	0*	0*	0*	0*	0	0
Bromus sterilis L.	Poaceae	0*	0*	10.18*	0*	0*	0*	0*	0*
Capsella bursa-pastoris L.	Brassicaceae	20.38*	0*	61.14*	0*	0*	0*	5.09*	0*
Cardaria draba (L..) Desv	Brassicaceae	61.14	0	30.56*	0*	0	0	0	0
Carduus pycnocephalus L.	Asteraceae	0	0	40.76	61.14	20.38*	5.09*	5.09*	0*
Carex divulsa Stokes	Cyperaceae	0*	0*	0	0	0*	0*	10.19	0
Carex grioletii Roem. ex Schkuhr	Cyperaceae	0	0	0*	0*	0	0	0	0
Centaurea sp.	Asteraceae	0	0	0	0	0	0	0*	0*
Chenopodium album L.	Chenopodiaceae	20.38	0	0	0	0	5.09	0	0
Convolvulus arvensis L.	Convolvulaceae	0*	0*	0*	0*	0	0	0*	0*
Coronilla varia L.	Fabaceae	0*	0*	0*	0*	0	0	0	0
Crataegus pseudomelano-carpa	Rosaceae	10.18*	20.38*	10.18	0	0*	0*	0	0
Crepis demavendi Bornm	Asteraceae	0	0	0	0	0*	0*	0*	0*
Crepis kotschyana Boiss	Asteraceae	193.6	132.46	71.32	10.18	91.71*	35.66*	30.57*	5.09*
Crepis willemetioides Boiss	Asteraceae	0	0	0*	0*	0*	0*	0*	0*
Dactylis glomerata L.	Poaceae	0*	0*	0*	0*	0*	0*	0	0
Dianthus orientalis Adams	Caryophyllaceae	0	0	0	0	15.28	5.09	56.04	10.19
Draba verna L.	Brassicaceae	142.66	10.18	234.36	81.52	56.04	0	25.47	0
Echium amoenum Fisch	Boraginaceae	10.18*	0*	0*	0	0	0	5.09	0
Erodium cicutarium L.	Geraniaceae	10.18	0	173.22	61.14	5.09*	15.28*	0*	0*
Eryngium caucasicum Trautv	Apiaceae	0*	0*	0*	0*	0*	0*	0*	0*
Filago vulgaris Lam	Asteraceae	0	0	0	0	0	0	0*	0*
Froriepia subpinnata (Ledeb.) Baill	Apiaceae	10.18	10.18	0	0	5.09*	0*	0	0
Fumaria vaillantii Loisel	Papaveraceae	10.18	40.76	40.76	20.38	5.09	0	0	10.19
Galium aparine L.	Rubiaceae	0	0	0	0	0	5.09	0	0
Galium humifusum M.Bieb	Rubiaceae	20.38*	10.18*	10.18*	40.76*	20.38*	0*	10.19*	0*
Galium songaricum Schrenk	Rubiaceae	40.76	0	30.57	0	208.89	76.42	0	5.09
Geranium pyrenaicum Burm	Geraniaceae	10.18	0	203.8	132.46	96.80*	40.76*	25.47	15.28
Gnaphalium luteo-album L.	Asteraceae	0	0	0	0	0*	0*	0*	0*
Hordeum glaucum Steud	Poaceae	0	0	0	0	0*	0*	0*	0*
Hypericum perforatum L.	Hypericaceae	713.3	662.34	1090.32	1131.08	173.23*	152.85*	81.52*	168.13*

Species	Family	Ungrazed area				Grazed area			
		Patch		Interpatch		Patch		Interpatch	
		0–5	5–10	0–5	5–10	0–5	5–10	0–5	5–10
Lathyrus chloranthus Boiss	Fabaceae	0*	0*	20.38*	0*	0	0	0	0
Lolium multiflorum Lam	Poaceae	0*	0*	0*	0*	0	0	0	0
Lolium perenne L.	Poaceae	0	0	0*	0*	0*	0*	0*	0*
Lonicera bracteolaris Boiss	Caprifoliaceae	50.94*	0*	0	0	0*	0*	0	0
Lycopus europaeus L.	Lamiaceae	0	0	0	0	10.19	10.19	40.76	10.19
Marrubium sp.	Lamiaceae	0*	0*	0*	0*	0*	0*	0*	0*
Marrubium vulgare L.	Lamiaceae	112.08	91.7	91.7	81.52	81.52	122.28	25.47	5.09
Medicago minima L.	Fabaceae	132.46	10.18	234.36*	112.08*	15.28*	0*	61.14*	10.19*
Medicago orbicularis (L.) Baryal	Fabaceae	0*	0*	30.56*	10.18*	50.95*	0*	15.28*	5.09*
Medicago polymorpha L.	Fabaceae	30.56*	0*	10.18*	20.38*	10.19*	0*	0*	0*
Medicago sativa L.	Fabaceae	0*	10.18*	20.38*	0*	0*	0*	0	0
Minuartia recurva Schinz & Thell	Caryophyllaceae	0	10.18	20.38	0	122.28*	35.66*	249.65*	45.85*
Nepeta cataria L.	Lamiaceae	50.94*	0*	0	0	0*	0*	0	0
Onobrychis sativa Lam	Fabaceae	0*	0*	0*	0*	0	0	0	0
Oxalis corniculata L.	Oxalidaceae	81.52	20.38	264.94	40.76	473.83*	203.80*	147.75	25.47
Papaver decaisnei Hochst.& Steud	Papaveraceae	10.18	0	122.28*	30.56*	127.37	101.9	208.89	25.47
Phleum bertolonii DC	Poaceae	0	0	0	0	0*	0*	0*	0*
Picris strigosa M.Bieb	Asteraceae	0*	0*	0*	0*	0	0	0	0
Plantago lanceolata L.	Plantaginaceae	0*	0*	438.16*	10.18*	15.28	0	30.57	0
Poa annua L.	Poaceae	10.18*	0*	0*	0*	0*	0*	0*	0*
Poa nemoralis L.	Poaceae	0*	0*	152.84	30.56	71.33*	0*	193.61	15.28
Poa pratensis L.	Poaceae	1650.78*	254.74*	2302.94*	560.44*	132.47*	25.47*	122.28*	20.38*
Polygonum aviculare L.	Polygonaceae	0	10.18	0	10.18	0	0	5.09*	0*
Potentilla reptans L.	Rosaceae	61.14*	10.18*	784.62*	438.16*	0	5.09	0*	0*
Prunus spinosa L.	Rosaceae	91.7*	50.94*	10.18	20.38	0*	0*	0	0
Pteridium aquilinum (L.) Kuhn	Dennstaedtiaceae	0	0	0	0	0*	0*	0*	0*
Ranunculus circinatus Sibth	Ranunculaceae	10.18	0	50.94	0	0*	5.09*	5.09*	0*
Rumex acetosa L.	Polygonaceae	0*	0*	0*	0*	0	0	0	0
Rumex sp.	Polygonaceae	30.56	0	10.18	0	61.14	10.19	0*	0*
Salvia verticillata L.	Lamiaceae	10.18	0	10.18	0	0	0	0*	0*
Sambucus nigra L.	Adoxaceae	0*	0*	0	0	0	0	0	0
Sanguisorba minor Scop	Rosaceae	0	0	0*	0*	0	0	0	0
Silene latifolia Poir	Caryophyllaceae	0*	0*	0*	0*	0*	0*	0	0
Sisymbrium loeselii L.	Brassicaceae	203.8	81.52	50.95	10.18	0	0	0	0
Stachys byzantina Boiss	Lamiaceae	0	0	0	0	0*	0*	0*	0*
Stachys persica S.G. Gmel	Lamiaceae	30.56*	0*	10.18*	0*	10.19*	5.09*	0*	0*
Stellaria media L.	Caryophyllaceae	203.8	30.56	927.28	611.4	407.60	219.08	499.31	112.09
Tamus communis L.	Dioscoreaceae	0	0	20.38	20.38	0	0	0	0
Taraxacum neospurium Soest	Asteraceae	0	0	0	0	10.19*	0*	10.19*	0*
Taraxacum serotinum Waldst	Asteraceae	0	0	0	0	5.09*	0*	0*	0*
Torilis arvensis (Huds.) Link	Apiaceae	0	0	0	0	0*	0*	0*	0*
Torilis radiata Moench	Apiaceae	10.18*	0*	0	0	5.09*	0*	20.38	0
Tournefortia sibirica L.	Boraginaceae	0	0	10.18*	0*	25.47*	0*	0	0

Species	Family	Ungrazed area				Grazed area			
		Patch		Interpatch		Patch		Interpatch	
		0–5	5–10	0–5	5–10	0–5	5–10	0–5	5–10
Tragopogon acanthocarpus Boiss	Asteraceae	0*	0*	0*	0*	0	0	0	0
Trifolium pratense L.	Fabaceae	0	0	0	0	5.09*	0*	0*	0*
Trifolium repens L.	Fabaceae	20.38*	0*	61.14*	61.14*	15.28*	15.28*	40.76*	0*
Trigonella monspeliaca L.	Fabaceae	0	0	0	0	0*	0*	0	0
Trisetum flavescens (L.) *P. Beauv*	Poaceae	0	0	0*	0*	0*	0*	0*	0*
Urtica dioica L.	Urticaeae	0	0	30.56	10.18	5.09*	5.09*	5.09	0
Valerianella uncinata Dufresne	Caprifoliaceae	0	0	0*	0*	0*	0*	0*	0*
Verbascum sp.	Scrophulariaceae	0*	0*	0*	0*	0	0	0*	0*
Veronica persica Poir	Plantaginaceae	50.94	10.18	50.94	71.32	922.19*	173.23*	1024.09*	81.52*
Vicia hirsuta (L.)Gray	Fabaceae	50.94*	10.18*	0*	10.18*	10.19	0	0	0
Viola odorata L.	Violaceae	81.52	10.18	30.56	0	81.52*	0*	0	0

References

Akiyama, T., & Kawamura, K. (2007). Grassland degradation in China: Methods of monitoring, management and restoration. *Grassland Science, 53*, 1–17.

Braz, M. I. G., Rodin, P., & Mattos, E. A. (2014). Soil seed bank in a patchy vegetation of coastal sandy plains in southeastern Brazil. *Plant Species Biology, 29*, 40–47.

Brown, B. J., & Ewel, J. J. (1987). Herbivory in complex tropical successional ecosystems. *Ecology, 68*, 108–116.

Callaway, R. M., Kikvidze, Z., & Kikodze, D. (2000). Facilitation by unpalatable weeds may conserve plant diversity in overgrazed meadows in the Caucasus Mountains. *Oikos, 89*, 275–282.

Cavieres, L. A., Badano, E. I., Sierra-Almeida, A., Gómez-González, S., & Molina-Montenegro, M. A. (2006). Positive interactions between alpine plant species and the nurse cushion plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile. *New Phytologists, 169*, 59–69.

Danet, A., Kéfi, S., & Meneses, R. I. (2017). Nurse species and indirect facilitation through grazing drive plant community functional traits in tropical alpine peatlands. *Ecology and Evolution, 7*, 11265–11276.

Erfanzadeh, R., Daneshgar, M., & Ghelichnia, H. (2020). Improvement of the seedling emergence method in soil seed bank studies using chemical treatments. *Community Ecology, 21*, 183–190.

Erfanzadeh, R., Hosseini Kahnuj, S. H., Azarnivand, H., & Pétillon, J. (2013). Comparison of soil seed banks of habitats distributed along an altitudinal gradient in northern Iran. *Flora, 208*, 312–320.

Erfanzadeh, R., Kamali, P., Ghelichnia, H., & Pétillon, J. (2016). Effect of grazing removal on aboveground vegetation and soil seed bank composition in sub-alpine grasslands of northern Iran. *Plant Ecology and Diversity, 9*, 309–320.

Erfanzadeh, R., Shahbazian, R., & Zali, H. (2014). Role of plant patches in preserving flora from the soil seed bank in an overgrazed high-mountain habitat in northern Iran. *Journal of Agricultural Science and Technology, 16*, 229–238.

Erfanzadeh, R., Shayesteh Palaye, A. A., & Ghelichnia, H. (2020). Shrub effects on germinable soil seed bank in overgrazed grasslands. *Plant Ecology and Diversity, 13*, 199–208.

Eskandarie, B. (2012). *Report on Iran's soil and agricultural status*. Country report on history and status of soil survey in Iran GSP regional workshop, Jordan, Amman, 1–5 April 2012.

Esmailzadeh, O., Hosseini, S. M., Tabari, M., Baskin, C. C., & Asadi, H. (2011). Persistent soil seed banks and floristic diversity in *Fagus orientalis* forest communities in the Hyrcanian vegetation region of Iran. *Flora, 206*, 365–372.

Falster, D. S., Duursma, R. A., & FitzJohn, R. G. (2018). How functional traits influence plant growth and hade tolerance across the life cycle. *Proceedings of the National Academy of Sciences, 115*, 6789–6798.

Filazzola, A., Liczner, A. R., Westphal, M., & Lortie, C. J. (2019). Shrubs indirectly increase desert seedbanks through facilitation of the plant community. *PLoS ONE, 14*(4), e0215988.

Ghahraman, A. (1986–2014). *Flora of Iran*. Institute of Forest and Grassland Research of Iran.

Giladi, I., Segoli, M., & Ungar, E. D. (2013). Shrubs and herbaceous seed flow in a semi-arid landscape: Dual functioning of shrubs as trap and barrier. *Journal of Ecology, 101*, 97–106.

Gonzalez, S. L., & Ghermandi, L. (2019). Dwarf shrub facilitates seedling recruitment and plant diversity in semiarid grasslands. *PLoS ONE, 14*(2), e0212058.

Howard, K. S. C., Eldridge, D. J., & Soliveres, S. (2012). Positive effects of shrubs on plant species diversity do not change along a gradient in grazing pressure in an arid shrubland. *Basic Applied Ecology, 13*, 159–168.

Hu, A., Zhang, J., Chen, X. J., Millner, J. P., Chang, S. H., Bowatte, S., & Hou, F. J. (2019). The composition, richness, and evenness of seedlings from the soil seed bank of a semi-arid steppe in northern China are affected by long-term stocking rates of sheep and rainfall variation. *The Grassland Journal, 41*(1), 23–32. https://doi.org/10.1071/RJ18025

Hupp, N., Llambí, L. D., Ramírez, L., & Callaway, R. (2017). Alpine cushion plants have species-specific effects on microhabitat and community structure in the tropical Andes. *Journal of Vegetation Science, 28*, 928–938.

Kent, M., & Coker, P. (1995). *Vegetation description and analysis, a practical approach*. Wiley.

Khaleghi, P. (1998). *The profile of the Caspian forests, research forest of Vazrud* (p. 380). Research Institute Forests and Grasslands.

King, E. G. (2008). Facilitative effects of *Aloe secundiflora* shrubs in degraded semi-arid grasslands in Kenya. *Journal of Arid Environments, 72*, 358–369.

Kottler, E. J., & Gedan, K. (2019). Seeds of change: Characterizing the soil seed bank of a migrating salt marsh. *Annals of Botany*. https://doi.org/10.1093/aob/mcz133

Li, C., Xiao, B., Wang, Q., Zheng, R., & Wu, J. (2017). Responses of soil seed bank and vegetation to the increasing intensity of human disturbance in a semi-arid region of Northern China. *Sustainability, 9*, 1–13.

Loydi, A., Zalba, S. M., & Distel, R. A. (2012). Vegetation change in response to grazing exclusion in montane grasslands, Argentina. *Plant Ecology and Evolution, 145*, 313–322.

Ma, M., Zhou, X., & Du, G. (2010). Role of soil seed bank along a disturbance gradient in an alpine meadow on the Tibet plateau. *Flora, 205*, 128–134.

McAuliffe, J. R. (1984). Sahuaro-nurse tree associations in the Sonoran Desert: Competitive effects of sahuaros. *Oecologia, 64*, 319–321.

Menezes, J. C., Cruz Neto, O. C., Azevedo, I. F. P., Machado, A. O., & Nunes, Y. R. F. (2019). Soil seed bank at different depths and light conditions in a dry forest in Northern Minas Gerais. *Floresta e Ambiente, 26*(2), e20170314. https://doi.org/10.1590/2179-8087.031417

Miller, G. R., & Cummins, R. P. (2003). Soil seed banks of woodland, heathland, grassland, mire and montane communities, Cairngorm Mountains, Scotland. *Plant Ecology, 168*, 255–266.

Mozaffarian, V. (2007). *A dictionary of Iranian plant names* (5th ed.). Farhang Moaser Press.

Niknam, P., Erfanzadeh, R., Ghelichnia, H., & Cerdà, A. (2017). Spatial variation of soil seed bank under cushion plants in a subalpine degraded grassland. *Land Degradation and Development, 29*, 4–14.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H. (2019). *Vegan: Community Ecology Package. R package version 2.5-5*. https://CRAN.R-project.org/package=vegan

Plue, J., Van Calster, H., Auestad, I., Basto, S., et al. (2021). Buffering effects of soil seed banks on plant community composition in response to land use and climate. *Global Ecology and Biogeography, 30*, 128–139.

Pugnaire, F. I., & Lazaro, R. (2000). Seed bank and understorey species composition in a semi-arid environment, the effect of scrub age and rainfall. *Annals of Botany, 86*, 807–813.

Ramirez, L. A., Rada, F., & Llambí, L. D. (2015). Linking patterns and processes through ecosystem engineering: Effects of shrubs on microhabitat and water status of associated plants in the high tropical Andes. *Plant Ecology, 216*, 213–225.

Rechinger, K. H. (1964). *Flora Iranica*. Akademische Druck-und Verlagsanstalt Graz.

Ren, J. Z., Hu, Z. Z., Zhao, J., Zhang, D. G., Hou, F. J., Lin, H. L., & Mu, X. D. (2008). A grassland classification system and its application in China. *Grassland Journal, 30*, 199–209.

Saatkamp, A., Poschlod, P., Venable, D. L. (2014). The functional role of soil seed banks in natural. In *Seeds: The ecology of regeneration in plant communities*. CAB International.

Sanou, L., Zida, D., Savadogo, P., & Thiombiano, A. (2018). Comparison of aboveground vegetation and soil seed bank composition at sites of different grazing intensity around a savanna-woodland watering point in West Africa. *Journal of Plant Research, 131*(5), 773–788. https://doi.org/10.1007/s10265-018-1048-3

Schonbach, P., Wan, H., Gierus, M., Bai, Y., Müller, K., Lin, L., Susenbeth, A., & Taube, F. (2011). Grassland responses to grazing: Effects of grazing intensity and management system in an Inner Mongolian steppe ecosystem. *Plant and Soil, 340*, 103–115.

Smit, C., Vandenberghe, C., Den Ouden, J., & Müller-Schärer, H. (2007). Nurse plants, tree saplings and grazing pressure: Changes in facilitation along a biotic environmental gradient. *Oecologia, 152*, 265–273.

Soliveres, S., Smit, C., & Maestre, F. T. (2015). Moving forward on facilitation research: Response to changing environments and effects on the diversity, functioning and evolution of plant communities. *Biological Reviews, 90*, 297–313.

Solomon, T. B., Snyman, H. A., & Smit, G. N. (2006). Soil seed bank characteristics in relation to land use systems and distance from water in a semi-arid grassland of southern Ethiopia. *South African Journal of Botany, 72*, 263–271.

Tessema, Z. K., Ejigu, B., & Nigatu, L. (2017). Tree species determine soil seed bank composition and its similarity with understory vegetation in a semi-arid African savanna. *Ecological Processes, 6*, 1–9.

Thompson, K. (2000). The functional ecology of seed banks. In M. Fenner (Ed.), *Seeds: The ecology of regeneration in plant communities* (pp. 231–258). CAB International.

Thompson, K., Bakker, J. P., & Bekker, R. M. (1997). *The soil seed banks of North West Europe: Methodology, density and longevity* (p. 276). Cambridge University Press.

Xie, L., Chen, W., Gabler, C. A., Han, L., Guo, H., Chen, Q., Ma, C., & Gu, S. (2016). Effects of grazing intensity on seed production of *Caragana stenophylla* along a climatic aridity gradient in the Inner Mongolia Steppe, China. *Journal of Arid Land, 8*(6), 890–898.