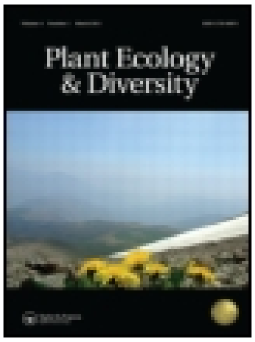

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ARTICLE

Shrub effects on germinable soil seed bank in overgrazed rangelands

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ABSTRACT

Background: Little information is available about the effects of different species of shrubs on the composition of the soil seed bank (SSB) and how the SSB could contribute to restoration of degraded grasslands.
Aims: We determined the role of three dominant shrubs on SSB characteristics and evaluated their potential for their possible use in rangeland restoration projects.
Methods: Ten sites, each containing three shrub species (*Onobrychis cornuta, Berberis integerrima* and *Juniperus sabina*) and a herbaceous patch (control) in close proximity, were sampled and their SSB density, richness and diversity were determined.
Results: Density of the SSB at 0–5 cm depth was lowest under *J. sabina* and highest under herbaceous vegetation, but did not differ between *B. integerrima* and *O. cornuta*. SSB density at 5–10 cm depth was significantly greater under *B. integerrima* than under the other shrubs or herbaceous patch. Species richness of the SSB was significantly greater under *B. integerrima* at 5–10 cm depth than under the other shrubs.
Conclusion: This study revealed that the extent to which vegetation affected SSB characteristics did not only depend on the presence of shrubs, but also on the species of shrub. We recommend *B. integerrima* as a priority species in restoration projects due to its significant positive influences on SSB.

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KEYWORDS
Canopy architecture; density and richness; seed bank; shrub patches; woody plants

Introduction

Livestock grazing is one of the most important land use impacts on ecosystems throughout the world, with ca. 47% of the world's land surface currently used by livestock; 80% of the grazing land is considered degraded (National Research Council 1994; Callaway et al. 2000). Overgrazing threatens the sustainability of pastoralist societies that depend on the forage production of rangelands, the functioning of the latter being linked to their structure and species composition (King 2008). Restoration of degraded pastures is therefore a priority. An approach that uses facilitator plants offers a promising strategy for restoration of degraded or overgrazed areas by the protection facilitators offer to other plant species from herbivores. Facilitation, whereby the presence of one plant species (e.g. shrubs) enhances the survival or fitness of other plants, has been documented in stressful environments, such as arid, saline, alpine and degraded areas (Callaway 1995; King 2008). For instance, the facilitative effects of *Aloe secundiflora* (King and Stanton 2008), *Guapira opposita* (Dalotto et al. 2018) and *Epacris gunnii* (Ballantyne and Pickering 2015) on other plants have been reported in stressful ecosystems. Facilitator plants, depending on the species, can significantly influence microhabitat conditions. Shrubs can create 'fertile islands' in grasslands by altering nutrient uptake, litter deposition and decomposition, burrowing animal activity, soil formation and erosion (Verdú and García-Fayos 2003; de Graaff et al. 2014; Keesstra et al. 2017) and soil seed bank (SSB) characteristics (Caballero et al. 2008; King 2008; Niknam et al. 2017). The development of such 'fertile islands' below and adjacent to individual shrubs is important in ecology since it could change both vegetation and soil characteristics (Chen et al. 2003). Indeed, the facilitator plants have been shown to affect the quality and quantity of soil microorganisms (Wardle and Zackrisson 2005), control the soil erosion and runoff rates (Zuazo and Pleguezuelo 2008; García-Ruiz et al. 2013; Keesstra et al. 2016) and influence SSB density and richness (Erfanzadeh et al. 2014b; Niknam et al. 2017; Funk et al. 2019). Some shrubs can be facilitators and alter the SSB under their canopies by trapping seeds or enhancing seed production by herbaceous species through increasing soil moisture, reducing erosion and adding litter to the soil surface (Ruiz et al. 2008; Olvera-Carrillo et al. 2009; Li et al. 2011; García-Sánchez et al. 2012; Mussa et al. 2016).

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Supplemental data for this article can be accessed here.

In addition, animals play an important role in the dispersal of seeds of many plants. Birds, ants, dung beetles and rodents physically carry the seeds to a new location (e.g. Vander Wall and Longland 2004; Hämäläinen et al. 2017). Woody plants offer shade, cover, food supply and nest sites for seed dispersers. Therefore, it can be assumed that interaction between woody plants with animals play a significant role in the spatial variation in SSB. However, different shrubs with different canopy architectures (erect stems or recumbent, broad-leaved deciduous or evergreen coniferous, broad or needle leaves) could have different efficiency in trapping seeds and could affect differently seed production by herbaceous species and therefore, they play different roles in changing the characteristics of SSB (density, richness and diversity). Nevertheless, none of the previous studies (e.g. Erfanzadeh et al. 2014b; Niknam et al. 2017) has focused on the effect of different species of shrubs on affecting SSB characteristics.

In this study, we selected three dominant shrub species and determined the density of SSB, richness and diversity in their understorey. Since the shrubs were different in their traits, including their architecture, we assumed that they could differently affect SSB characteristics. We hypothesised that species with a relatively open canopy (in our case *Berberis integerrima* and *Juniperus sabina*) would be associated with a greater density, species richness and diversity of seeds by allowing greater penetration of wind and water, and greater *in situ* production by herbaceous species compared to other shrubs with closed canopies such as the hemispherical cushion-forming *Onobrychis cornuta*. In addition, we estimated the similarities of the SSB composition among patches dominated by the three shrubs and outside of the patches, dominated by herbaceous species. Finally, we compared the composition of soil seed bank and above-ground vegetation. Regarding the restoration of rangelands, this study offers a contribution to understanding and quantifying the roles different shrub species have on SSB and for its potential use for recovery of degraded sites. By identifying species with great capacity to accumulate a rich SSB could be then used plant restoration projects.

Additionally, the SSB characteristics were estimated and compared between two soil depths (0–5 cm and 5–10 cm). The density and species richness of SSB are usually highest at the soil surface because of highest seed input (Erfanzadeh et al. 2010). Nevertheless, sometimes peak densities or species diversities of SSB occur in deeper soil layers or remain constant along the soil depth gradient due to special environmental conditions (stresses and disturbances) (e.g. Espinar et al. 2005). In our study, the environmental conditions (temperature, fertility, humidity) were taken to be different between beneath the shrubs and adjacent open area (herbaceous patch) and, beneath the shrubs with open canopy and with dense canopy (García-Sánchez et al. 2012; Mussa et al. 2016). Therefore, it might be assumed that the vertical distribution of seed densities and diversities could be different between beneath the different shrubs and herbaceous patches.

Materials and methods

Study sites and field methods

The study was conducted in Baladeh Watershed, Mazandaran province, Iran (36° 16′ 30″ N – 36° 18′ 19″ N; 51° 49′ 30″ E – 51° 51′ 17″ E) at elevations between 2844 and 2963 m a.s.l. The average annual rainfall was 394 mm and mean annual temperature 5.5°C (Khaleghi 1998).

Sheep are the dominant grazers in the region, with a few goats (ca. five heads of sheep and/or goats per ha), from April to September each year. Heavy grazing has led to locally exposed soil. Using of native plants for revegetating bare soil and restoration of degraded sites is a priority. SSB has been considered one of the major natural sources that facilitates the recovery of degraded vegetation (Shang et al. 2016). We hypothesised that shrubs played an important role in maintaining and increasing of SSB above that in open areas. We carried out this study to quantify the potential of shrub species to increase the SSB associated with them and thus their potential use for restoration. Our observations in recent years and personal communication with native pastoralists have indicated that the density of shrubs (particularly that of *Berberis*) in the past had been larger than it is today. Therefore, it is important to restore firstly shrubs that associated with larger and richer SSB and secondly, consider restoring shrub species with higher grazing value (see also Erfanzadeh et al. 2014a).

Three common and dominant shrub species with different canopy architectures and, adjacent herbaceous vegetation as control (herbaceous patches) were selected. *Berberis integerrima* Bunge (Berberidaceae), is a deciduous shrub with vertical stems and, an average height and canopy diameter of 1.8 m and 1.5 m, respectively. The species has multiple stems and an open canopy characterised by large spaces among thorny branches. The species is palatable and is being grazed intensively in the study area. It has an estimated density of 12 individuals ha^{-1} and a cover of 5%. *Juniperus sabina* L. (Cupressaceae), is a shrubby evergreen dwarf conifer. It is a wide-spreading shrub growing to an average height of ca. 0.9 m. It has a procumbent canopy with empty spaces between the branches. The shoots or stems arise from a main axis (as of a tree) and trail along the ground without rooting. This species is unpalatable, and its density is ca. 30 individuals ha^{-1} and has a cover of 10%. Previous studies have shown that this dioecious species has different effects on soil parameters and above-ground vegetation depending on the gender (Verdú and García-Fayos 2003; Verdú et al. 2004). In this study, we selected the individuals randomly without considering the gender. *Onobrychis cornuta* (L.) Desv. (Fabaceae) is a perennial, hemispherical thorny cushion shrub with deciduous leaves and spiny branches. It forms dense, compact cushions or mats that can extend laterally for >1 m and reach 60 cm in height. This species is a palatable legume with relatively high protein. It has a density of 160 individuals ha^{-1} and covers an average of 20% the area (Khaleghi 1998). Herbaceous vegetation covers 50% the area, dominated by perennial grasses such as *Festuca ovina* and *Bromus tomentellus*.

We randomly selected 10 replicate sampling areas, each containing the three shrub species and a herbaceous patch (control) in close proximity to each other (Figure 1). Sampling areas were separated by distances of 50 m to 600 m. The distance between any two sampling areas was at least 50 m to exclude spatial autocorrelation. Soil texture was light and sandy with an average depth of 50 cm, consisting of A and C horizons (Khaleghi 1998). Soil sampling was conducted in early autumn 2016, after seed dispersal. Thus, the germinable seeds contained transient and persistent components of the SSB. In each sampling area, in each individual patch, after removing coarse litter (>2 cm) 10 soil cores (subsamples) were collected at random, to a depth of 10 cm, with a 5 cm diameter auger. Each subsample was divided into two sections (0–5 and 5–10 cm) and subsamples were then pooled per depth for each patch. The soil samples were transported to the laboratory and were stored at ca. 4ºC for cold stratification for a period of 1 month (Miller and Cummins 2003).

Subsequently, soil samples were transported into the greenhouse of the Faculty of Natural Resources, Tarbiat Modares University and each sample was spread over a mix of (1:1) sterilised potting soil and sand of a thickness of 3 cm in free-draining plastic trays of 25 cm × 35 cm (totally 80 trays). Eight control trays containing only sterile potting soil and sand, were placed at random with the samples to test for contamination of samples from greenhouse or nearby seed sources. All trays were kept under natural light and temperature conditions and were watered to keep them moist (Niknam et al. 2017). Air temperature varied between 14°C and 25°C. Germinated seedlings were identified, counted and removed once they reached an identifiable stage. Seedlings that could not be identified immediately were transplanted to pots to allow further growth until identification was possible. Two seeds of *Celosia* sp. were germinated in all control trays. Since *Celosia* sp. is an ornamental plant that grows in front of the greenhouse, we ignored its seedlings in the trays.

After a germination period of 6 months, no further seedlings were observed. Therefore, the trays were left to dry for 2 weeks and then the samples were rewetted and kept for another 21 days to encourage seed dormancy breaking (six seeds including three herbaceous species germinated). At the end, the residual soil was partly combed for possible remaining seeds using

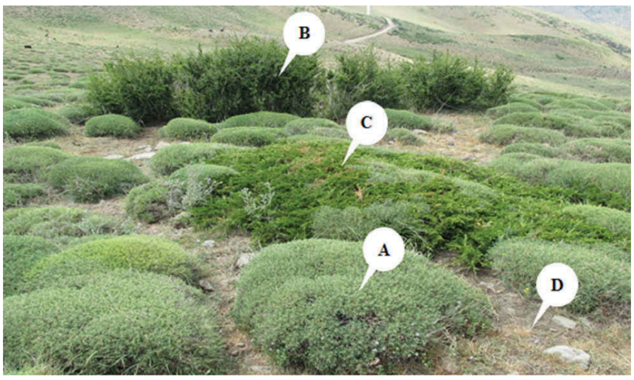

Figure 1. Sampling areas had three shrub species of *Onobrychis cornuta* (a), *Berberis integerrima* (b) and *Juniperus sabina* (c) that formed woody patches in the surrounding herbaceous vegetation, used as control (d) for comparing soil seed bank density and composition, Baladeh Watershed, Mazandaran province, Iran (36° 16′ 30″ N – 36° 18′ 19″ N; 51° 49′ 30″ E – 51° 51′ 17″ E).

a binocular microscope in randomly selected trays (Erfanzadeh et al. 2014a). Since the number of seeds that remained in the investigated soil samples was negligible (i.e. zero or one seed in a few trays), this procedure was not repeated for all trays.

The density of SSB was expressed as the number of seeds per m^2 and SSB richness was measured as the number of species for each compound soil sample. Finally, the Shannon diversity index was calculated for each soil sample according to Hubálek (2000).

During June and July 2017, we recorded the presence of all plant species within each of the patches sampled for SSB. Species abundance of the above-ground vegetation was not estimated because it was not possible to place a sampling frame beneath the shrubs and we used presence-absence data for above-ground vegetation in the analyses.

Statistical analyses

The normality of the data was examined using the Kolmogorov-Smirnov test. Seed density was square-root-transformed to meet normal distribution; other variables were not transformed. The effects of patch quality (shrub species and herbaceous) and depth categories (subplot) on the seed bank characteristics (seed density, species richness and Shannon diversity) were determined using general linear models with a split plot design. There were two levels of units in our sampling design the patch representing a block while the depth categories were treated as split plots. Therefore, a split-plot design was applied for the analysis of the data. Means were compared using Tukey HSD multiple comparison at $\alpha = 0.05$ level.

One-way ANOVA tests were used to compare total SSB density (0–10 cm), total species richness (0–10 cm) and total Shannon diversity (0–10 cm) among different patches (three shrub patches and herbaceous patch). All statistical analyses were made using SPSS v. 17.

To compare the composition and abundance of species in the SSB among the four patch types, an ordination was carried out using non-metric multidimensional scaling (NMDS). For the NMDS, relative abundance (relative density) were calculated as the number of seedlings emerged of a species divided by the total number of seedlings in that emerged from the seed bank for each individual sample.

In addition, we compared SSB and above-ground vegetation compositions using an additional NMDS. We considered the data from all three types of shrub patches as one group for SSB and for above-ground vegetation as well. Therefore, four groups were constructed: one group with 30 replicates for SSB under shrub patches, one group with 30 replicates for above-ground vegetation under shrub patches, one group with 10 replicates for SSB under herbaceous patches and one group with 10 replicates for above-ground vegetation under herbaceous species. For both SSB and above-ground vegetation, the presence-absence data of species were used. The ordinations were conducted using the package 'vegan' (Oksanen et al. 2019) in R (R Core Team 2018). Similarity matrices were calculated using the Bray-Curtis coefficient. The scores on the first two axes of NMDS were also compared using one-way ANOVA.

Results

Soil seed bank and vegetation composition

In total, 6,568 seedlings of 61 species, belonging to 22 families germinated from the soil samples: 2,086 seedlings of 38 species herbaceous patch; 1,973 seedlings belonging to 48 species in the *B. integerrima* patch; 1,525 seedlings belonging to 41 species in the *O. cornuta* patch; and 984 seedlings belonging to 36 species in the *J. sabina* patch. Twenty-two species were common to the four patch types. The highest number of common species were found between *B. integerrima* and herbaceous patches and the lowest between *J. sabina* and herbaceous patches (Table S1).

In total, 120 species were found in the above-ground vegetation and SSB combined. Thirty-three species that were present in the SSB were absent in the vegetation, and 59 species present in the vegetation were absent from the SSB. Most species were observed under the *B. integerrima* (Table S1). Asteraceae and Poaceae had the greatest number of species in the SSB. The seedlings of *O. cornuta* and *B. integerrima* emerged from the soil samples but not of *J. sabina*.

Variation of soil seed bank characteristics among the patches and depths

The density of SSB was significantly different among patch types and between depths (Table 1; Figure 2). Seed density in the upper soil layer (0–5 cm) was lowest under *J. sabina* (3,898 seeds m^{-2}) and highest under the herbaceous patches (9,737 m^{-2}). At 5–10 cm depth, seed bank density was highest under *B. integerrima* (2823 seeds m^{-2}) (Table 1; Figure 2). Total density (0–10 cm) was highest in the herbaceous and *B. integerrima* and lowest in *J. sabina* patches (df = 3, F = 3.01 and $P = 0.04$) (Figure 2).

Table 1. Results of a split-plot ANOVA comparing effects of patch (three different shrub species and herbaceous vegetation) and depth of sampling on soil seed bank density, Baladeh Watershed, Mazandaran province, Iran (36° 16′ 30″ N – 36° 18′ 19″ N; 51° 49′ 30″ E – 51° 51′ 17″ E). ANOVA was conducted using square-root transformed values of soil seed bank densities.

Source of variation	SS	df	MS	F
Main-plot (Patch)	3904.89	3	1301.63	2.94*
Main-plot error	15,917.04	36	442.14	
Sub-plot (depth)	43684.65	1	43684.65	212.65**
Main-plot and sub-plot interaction	3705.83	3	1235.28	6.01**
Sub-plot error	7395.49	36	205.430	
Total	74607.91	79		

* significant at α = 0.05; ** significant at α = 0.01.

Species richness of the SSB was significantly different among patch types at 5–10 cm (highest under *B. integerrima*), but not at 0–5 cm (Table 2; Figure 3). At 0–10 cm it was higher under *B. integerrima* than under the rest (df = 3, F = 3.8, $P = 0.04$; Figure 3). The values of H' were significantly different between depths (Table 3; Figure 4) but not among patches; no differences were found at 0–10 cm.

Similarity of soil seed bank composition between the four patches

Analysis of variance (ANOVA) results of SSB sample scores on the first (df = 3, F = 13.96, $P < 0.01$) axis were significantly different but not on the second axis (df = 3, F = 2.60, P-value = 0.07). SSB samples of herbaceous patches were clearly distinct from those of the *J. sabina* and those of *O. cornuta* from samples of the *B. integrrima* (Figure 5).

NMDS of species/presence data illustrated that a clear separation of the species composition of SSBs from vegetation composition occurred for shrubby patches and also for herbaceous patches (along axis 1: df = 3, F = 10.31 and $P < 0.01$) (Figure 6).

Table 2. Results of a split-plot ANOVA comparing effects of patch (three species of shrubs and herbaceous vegetation) and depth on species richness of soil seed bank, Baladeh Watershed, Mazandaran province, Iran (36° 16′ 30″ N – 36° 18′ 19″ N; 51° 49′ 30″ E – 51° 51′ 17″ E) at elevations between 2844 and 2963 m a.s.l.

Source of variation	SS	df	MS	F
Main-plot (patch)	90.05	3	30.02	2.89*
Main-plot error	373.5	36	10.38	
Sub-plot (depth)	1344.8	1	1344.80	146.04**
Main-plot and sub-plot interaction	35.7	3	11.90	1.29ns
Sub-plot error	331.5	36	9.21	
Total	2175.55	79		

* significant at α = 0.05; ** significant at α = 0.01; ns: not significant.

Discussion

This study showed differences in the richness and abundance of the soil seed bank (SSB) associated with the different shrub species in a semiarid montane rangeland. Combined the fact that *B. integerrima* is a palatable shrub and has a larger and more diverse SSB than the other two species argue for its prioritisation in the restoration of degraded areas of the rangeland. We expected that the open canopy in *B. integerrima* would give an enhanced opportunity to herbaceous species for growing and producing seeds in the empty spaces inside the shrub patches. Indeed, our results showed that SSB density under *B. integerrima* was higher than under *O. cornuta* (not significant at 0–5 cm) or *J. sabina*. We argue that probably the open canopy of *B. integerrima* appears to increase the density of SSB, particularly the persistent component in the deeper soil layer. Comparing with *B. integerrima*, less divers and smaller SSB under *O. cornuta* indicated that the procumbent, dense, and compact canopy of *O. cornuta* should restrict seed inputs, and limit the growth and reproduction of herbaceous species under it. Therefore, seed density and richness beneath *O. cornuta* became less than beneath *B. integerrima* and less than outside its canopy as well.

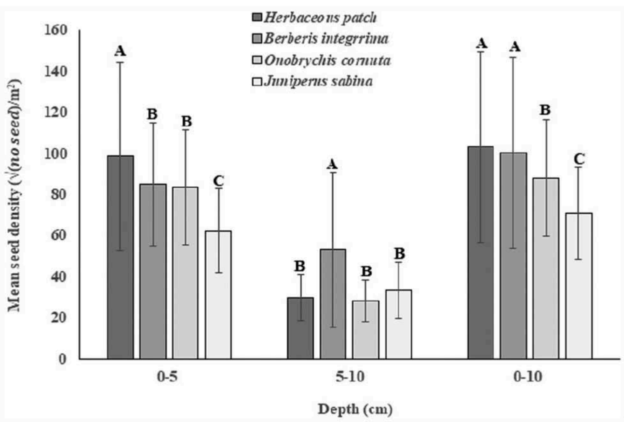

Figure 2. Mean (± SE) densities of seeds that germinated under three shrubs: *Onobrychis cornuta, Berberis integerrima* and *Juniperus sabina* and herbaceous vegetation, Baladeh Watershed, Mazandaran province, Iran. Upper case letters indicate statistically significant differences ($P < 0.05$) among patch types within each soil layer.

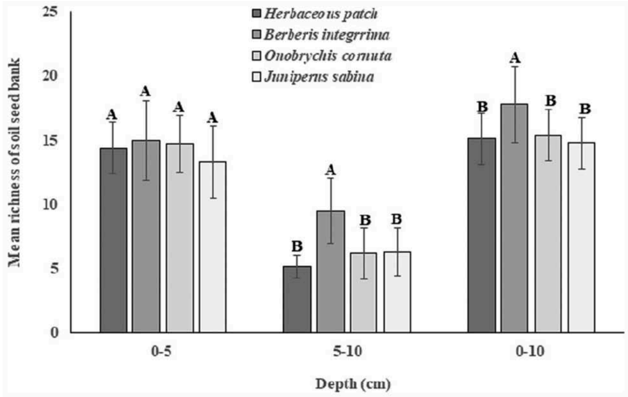

Figure 3. Mean (± SE) species richness of germinants under three shrubs: *Onobrychis cornuta, Berberis integerrima* and *Juniperus sabina* and herbaceous vegetation, Baladeh Watershed, Mazandaran province, Iran. Upper case letters indicate statistically significant differences ($P < 0.05$) among patch types within each soil layer.

Table 3. Results of a split-plot ANOVA comparing effects of patch (three species of shrubs and herbaceous vegetation) and depth on Shannon diversity index of the soil seed bank, Baladeh Watershed, Mazandaran province, Iran (36° 16′ 30″ N – 36° 18′ 19″ N; 51° 49′ 30″ E – 51° 51′ 17″ E).

Source of variation	SS	df	MS	F
Main-plot (patch)	0.574	3	0.191	1.92ns
Main-error	3.586	36	0.1	
Sub-plot (depth)	4.097	1	4.097	32.41**
Main-plot and sub-plot interaction	0.448	3	0.149	1.181ns
Sub-plot error	4.551	36	.126b	
Total	13.256	79		

* significant at α = 0.05; ** significant at α = 0.01; ns: not significant.

Finally, *J. sabina* with its open canopy had a lower SSB density (0–5 cm and 0–10 cm) than the other two shrubs and outside the canopy. Thus, in the case of *J. sabina*, factors other than canopy architecture might be involved in having a less dense SSB in relation to the other species. Some species of *Juniperus* and other conifers (e.g. *Pinus halepensis*) have been shown to have allelopathic effects on herbaceous species (e.g. Fernandez et al. 2006; Young and Bush 2009) by possessing phenolic compounds, monoterpenes, benzoic and cinnamic acid (Kil 1992). Therefore, the combination of limited seed production caused by allelochemicals and impeded extraneous input caused by the closed canopy are likely to cause a major decrease in the density of the SSB under *J. sabina*. As a result, the canopy architectures alone of shrubs, does not determine SSB characteristics. In a previous study, we have found that higher seed density around the canopy of woody species was related to seed input through production of seed by herbaceous species in situ rather than by seed trapping in the canopy (Niknam et al. 2017).

In agreement with some other studies (Marone et al. 2004; Caballero et al. 2008; Braz et al. 2014; Erfanzadeh et al. 2014a; Niknam et al. 2017; Tessema et al. 2017), our results showed a relatively high seed number and richness buried in soil at 5–10 cm and 0–10 cm depths under *B. integerrima* compared with the control area devoid of shrubs. Generally, shrub patches in a herbaceous species matrix increase seed bank density, overall richness and diversity. Previous work has reported that local accumulation under shrubs was the result of seed input received via wind and water and

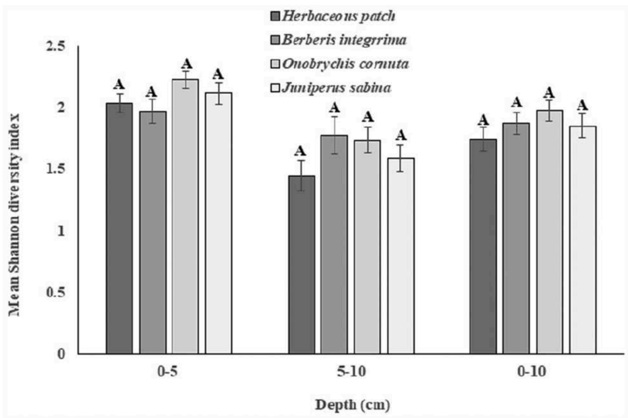

Figure 4. Mean (± SE) Shannon diversity index under three shrubs: *Onobrychis cornuta, Berberis integerrima* and *Juniperus sabina* and herbaceous vegetation, Baladeh Watershed, Mazandaran province, Iran. Upper case letters indicate statistically significant differences ($P < 0.05$) among patch types within each soil layer.

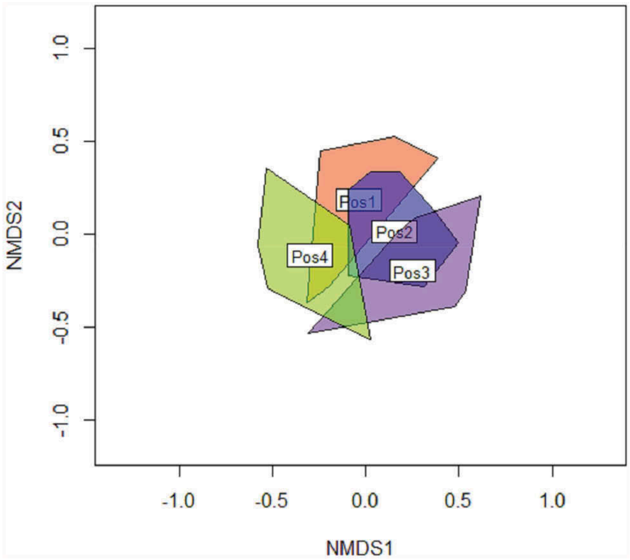

Figure 5. Non-metric multidimensional scaling of soil seed bank (SSB) composition (0–10 cm) under three shrubs: *Onobrychis cornuta* (Pos1), *Juniperus sabina* (Pos2), *Berberis integerrima* (Pos3) and herbaceous vegetation (Pos4), Baladeh Watershed, Mazandaran province, Iran. n = 40 (patch types × sites); R^2 = 0.93 for non-metric fit, R^2 = 0.57 for linear fit; stress = 0.04).

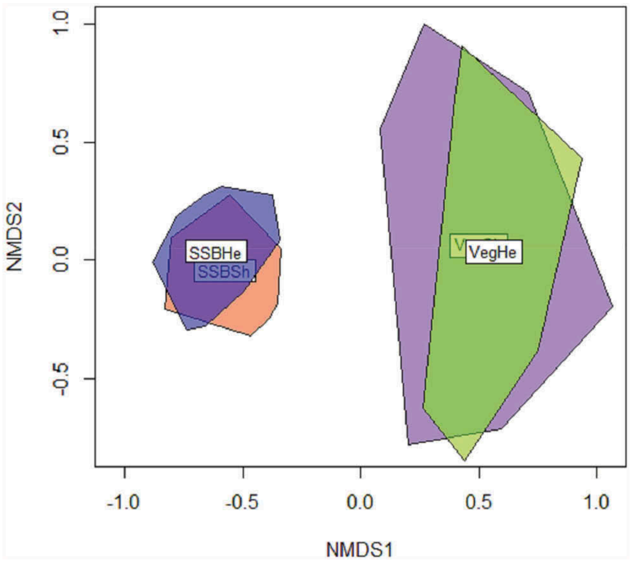

Figure 6. Non-metric multidimensional scaling (NMDS) of species composition of above-ground vegetation and the soil seed bank (presence-absence data). R^2 = 0.96 for non-metric fit; R^2 = 0.83 for linear fit; stress = 0.02). SSBSh: soil seed bank under shrub patches; SSBHe: soil seed bank under herbaceous patches; VegSh: above-ground vegetation under shrub patches; VegHe: above-ground vegetation under herbaceous patches.

trapping beneath woody patch and seed producing by smaller plant species within patch (Bullock and May 2004; Pekas and Schupp 2013; Braz et al. 2014; Erfanzadeh et al. 2014a; Tessema et al. 2017). Birds can contribute too to the transport of seeds, and shrub species that offer perches and food may contribute to recruiting zoochorous species to the SSB (Spiegel and Nathan 2007). In addition, amenable soil conditions beneath the patches may facilitate colonisation and growing of herbaceous species and increase seed production by these species. However, seed density in the surficial layer (0–5 cm) were higher in the herbaceous patches than beneath the canopy of any shrub in our study. The data showed that 65% of the seeds of the upper soil layer (0–5 cm) that germinated from samples collected in herbaceous patches belonged to three species: *Stellaria media*, *Hypericum hyssopifolium* and *Senecio vernalis*. Since these species have a capability of high seed production (Salisbury 1961; Stace 1997; Esmailzadeh et al. 2011; DiTomas and Kyser 2013; Erfmeier et al. 2013; Hantsch et al. 2013) and are unpalatable or toxic for grazers (e.g. Eröksüz et al. 2003; Burrows and Tyrl 2013), therefore high level of seed production in these unpalatable species probably increased the number of seeds in areas grazed heavily, outside of the protection of shrubs. In addition, in our study, the fact that we sampled in the autumn, after seeds had been dispersed, the upper soil layer in the herbaceous patches probably included seeds of these three species that would not have penetrated enough into the soil and would have not been lost through decay, predation, or runoff.

Soil seed bank density, richness and diversity showed a decreasing trend with depth, being significantly higher in the upper layers than in the lower layers in all type of patches, also found in other studies (e.g. Erfanzadeh et al. 2010; Ma et al. 2010; Niknam et al. 2017). Although many factors including seed size, seed shape and environmental condition affect the depth that seeds are able to penetrate (Thompson et al. 2001), the majority of viable seeds are concentrated in the first few centimetres of the soil (see also Erfanzadeh et al. 2016). Surprisingly, *O. cornuta* and *B. integerrima* were found in the SSB while the seeds of *J. sabina* were absent. Lack of sexual reproduction of *J. sabina* was reported in some habitats (e.g. Wesche et al. 2005 within mountain steppe populations in semi-arid southern Mongolia) and therefore, low reproduction by seeds might be involved in the absence of SSB of this shrub.

The results of the NMDS ordination indicated that SSB composition differed between herbaceous and shrub patches. In addition, NMDS revealed greater difference between the floristic composition of the SSB and above-ground vegetation than between the SSB samples or above-ground vegetation types (shrub vs. herbaceous). Many species, such as *Achillea vermicularis, Alchemilla vulgaris* and *Centaurea cyanus* were absent from the seed bank while they were frequent in the above-ground vegetation. Most of these species are perennial, and they, especially the shrubby ones, are well known for their transient seed bank (Thompson et al. 1997). Moreover, perennials probably increased their vegetative growth as an alternative form of reproduction under grazing and therefore contributed less to the seed bank. Low similarity between SSB and above-ground vegetation have been reported by other researchers (Díaz-Villa et al. 2003; Erfanzadeh et al. 2013; Tessema et al. 2017).

Conclusions

The extent to which vegetation affects soil seed bank (SSB) parameters is not only dependent on the presence of shrubs, but also on the species of shrubs. In this study, *B. integerrima* shrub patches appeared to be the best candidate to maximise the SSB. Since the conservation of mature shrubs of dominant species is of paramount importance for ecological stability and possible restoration of degraded area, we recommend *B. integerrima* as a priority species in conservation projects aimed at restoring semiarid montane rangelands in the distribution area of the species. This species showed the highest SSB density and richness under the canopy, therefore, combined with its high grazing value, could be considered for revegetating of bare areas.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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