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Effect of burning of evergreen savin juniper and herbaceous patches on soil: Seed banks, chemical and biological properties

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ABSTRACT

The coniferous shrub species *Juniperus sabina* (savin) is widespread in mountainous regions of Eurasia. The species produces large amounts of fire-prone plant mass in its habitats. The aim of this study was to assess the effect that burning of savin shrubs has on the soil seed bank (SSB), the microbial respiration and the amount of organic matter under its canopy. In each of three sampling areas, four individuals of savin were randomly selected. Under each of these individuals and on adjacent herbaceous control patches, soil samples were taken from 0 to 5 cm and 5–10 cm depths for SSB, biological and chemical analyses. The sampling was repeated after burning the canopy. We found that the immediate effects of burning on the SSB and on the biological and chemical soil parameters were significantly negative. In particular, SSB density, magnitude of microbial respiration and amount of organic matter were significantly decreased after savin canopy burning in 0–5 cm depth, while these changes were less pronounced on the burned herbaceous patches. Hence the restoration of gaps created by burning savin cannot rely on the SSB. Furthermore, alkalization of the soil and decreased soil quality caused by savin burning might hamper the vegetation recovery even in the medium to long run.

1. Introduction

Grasslands are among the most widespread terrestrial ecosystems on earth, covering about 40% of the earth's surface, and provide numerous ecosystem services to human society (Lyu et al., 2020). These ecosystems are important for the conservation of flora and fauna from local to landscape level and in many cases represent hotspots of biodiversity (Wilson et al., 2012; Habel et al., 2013). The loss of their biodiversity can compromise the functioning of ecosystems and sustained ecosystem services the human society depends upon (Wagg et al., 2021). Studies on sustaining aboveground grassland biodiversity and spatial dispersal of species are numerous, whereas the temporal aspects of seed dispersal (i.e. the formation of soil seed banks) are less frequently studied (Török et al., 2020). The soil seed bank (SSB) and microbial communities are among the most crucial drivers in conserving grassland biodiversity. The SSB is an accumulated repository of viable seeds in the upper soil layers of a specific area. It forms an ecological memory, which reflects the

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management history and the vegetation composition in the past (Zou et al., 2021). The study of the SSB is important for population and vegetation ecology as it plays a key role in vegetation dynamics and floral diversity (Ghasempour et al., 2022). Some other soil properties like soil respiration (i.e. CO_2 emission from soil) are active indicators of diversity and magnitude of microbial communities, which reflect the soil health and are directly related to soil ecosystem productivity and biodiversity (Freidenreich et al., 2021).

Fire is a powerful driver of ecological functions and services, which affects organismal traits, population sizes, species interactions, community compositions, carbon and nutrient cycling and ecosystem functioning in grasslands (McLauchlan et al., 2020). Several factors affect the behaviour of fire. For instance, topography is an important determinant of fire development (Storey et al., 2021), and meteorological conditions such as humidity and air temperature have a direct effect on the probability of wildfires (Sadat Razavi et al., 2022). However, it was reported that among the main factors that determine the behaviour of fires, quality and quantity of the fuel load could be the most important ones (Stavi, 2019). In this regard, the availability of fuel in grasslands is low compared to forests, and so is the fire intensity in these types of open habitats (Stavi, 2019); however, fuel availability and subsequently fire intensity vary between sites or even patches depending on whether woody or herbaceous vegetation dominates. In grasslands the fire intensity under the canopy of shrubs is higher than in open areas, and this could have significant effects on both soil parameters and soil seed bank composition and density because fire is one of the major drivers linked to soil parameters in grasslands such as SSBs and microbial respiration (Fernandes et al., 2021). Given the importance of SSBs in the recovery and restoration of biodiversity in areas disturbed by fire, the effects of fire on SSBs have been extensively studied in different grasslands (e.g. Kiss et al., 2018 and de Oliveira et al., 2019 in grasslands; Cuello et al., 2020 in temperate grasslands), and the results showed that fire affected the frequency and composition of SSBs significantly. In some fire-prone habitats the conditions for seed germination and seedling establishment from SSBs become particularly favourable immediately after a fire (Ghasempour et al., 2022). Consequently, many plants contribute to the SSBs only when they have been released from dormancy by a fire event, i.e. after being exposed to fire-related clues such as heat and smoke (Luna, 2020). However, many studies dealt with Mediterranean ecosystems, where fire is considered an essential structuring force of plant communities (e.g., Céspedes et al., 2012; Manela et al., 2019; Luna, 2020; Ugarte et al., 2021). Moreover, the effect of fire on grasslands has usually been studied by comparing unburned sites with burned ones one to several years after burning (Konsam et al., 2020; Lipoma et al., 2018). The extent to which fires may affect SSBs in other grasslands and immediately after burning is scarcely studied (e.g., de Andrade and Miranda, 2014).

Soil respiration is sensitive to burning and can be severely disturbed by fire (Hu et al., 2021). Former studies have shown that fire affected soil respiration directly by influencing the microbial activity in the soil (e.g., Holden et al., 2015) and indirectly by changing some chemical soil properties such as pH, nutrient availability and organic matter, which are all related to soil microorganisms (Throop et al., 2017). However, the extent to which fire disturbance affects soil respiration might depend on the intensity and the duration of the fire. For example, high temperatures during a fire significantly reduced microbial activity and respiration in soil (Baker and Bogorodskaya, 2010; Sun et al., 2014; Ludwig et al., 2018; Vourlitis et al., 2022). Conversely, other studies have shown that fire resulted in greater nutrient availability and thus promoted soil microbial respiration (Goberna et al., 2012; Stirling et al., 2019; Hu et al., 2021). Some researchers concluded that prescribed fire induced no changes in soil respiration immediately after the fire (Plaza-Álvarez et al., 2017). So, the complex responses of microbial respiration to fire disturbance led to contradictory results in estimating post-fire respiration levels in ecosystems. Moreover, to our knowledge there is no information available on the effect that burning of a particular shrub species has on soil respiration underneath its canopy.

Similar to the SSB and respiration, soil organic matter (SOM) forms a basis for healthy and productive soils (Lehmann et al., 2020). SOM has major impacts on multiple soil properties and functions such as enhancing water-holding capacity and infiltration, improving soil structure and stability, reducing soil bulk density and decreasing water runoff and soil erosion (Ferreira et al., 2022). SOM is the largest terrestrial store of carbon on earth and helps to regulate our climate (Berryman et al., 2020). In addition, soils with adequate levels of SOM provide a suitable habitat for microorganisms, resulting in high soil biodiversity. An important function of grasslands is the sequestration and storage of SOM. Therefore, several studies focused on the effects of environmental factors on SOM in grasslands with frequent wild and prescribed fires (e.g. Neary and Leonard, 2020; Pellegrini et al., 2022). Most of these studies showed a significant effect of fire on SOM, but the direction in which SOM was changed varied between the studies. Some authors reported a decrease in SOM after fire (e.g., Abdalla et al., 2021 at 0–5 cm soil depth), while others found no significant change or even an increase of SOM (e.g., Novara et al., 2013 at 0–5 cm soil depth). These discrepancies are likely due to the large number of interacting factors, which makes for a highly variable effect of fire. Hence variations of SOM between and within shrub patches after fire might have occurred and just not been studied.

Juniperus species are evergreen trees and shrubs of the Cupressaceae family. The genus is considered the most diverse within its family, and its species are widely distributed in the Northern Hemisphere (Adams, 2014). The large distribution range of juniper species is mainly due to their tolerance to extreme environmental factors (Mathaux et al., 2016) allowing them to adapt to very different habitats. Indeed, species of this genus are found from sea level to high altitudes, in forests and deserts, on rocky cliffs and sand dunes (Farhat et al., 2020). *Juniperus sabina* L. (hereafter savin) is a mountainous species, so that its extended distribution range covering a vast area of Eurasia, from Spain in the West to Mongolia and Siberia in the East, is restricted to higher altitudes and therefore fragmented (Adams et al., 2016). In Iran savin is naturally distributed in many areas of the Alborz mountainous grasslands in the North of the country, from Astara in the Northwest to Gorgan in the Northeast. The shrub species plays an important role in arid and semi-arid areas, where it benefits the environment by preventing land desertification and soil erosion and by saving organic carbon and protecting the soil seed bank (Erfanzadeh et al., 2020). In addition, savin contains chemical components such as camphor and podophyllotoxin, which have an insecticidal effect and can also be used as medicine for treating diseases such as rheumatoid arthritis (Xu et al., 1991; Sadeghi-Aliabadi et al., 2009). The species is also able to produce large amounts of bioactive compounds, mainly essential oils such as terpenoids (Rajcevic et al., 2022). These substances are volatile and highly flammable so that occurrences of savin increase the probability of wildfires.

In savin habitats in Iran, wildfires and arsons have been reported as a frequent event for a long time. For example, in the Golestan National Park in Alborz, where this species is dominant in most high elevation areas, 67 large fires occurred between 1957 and 1997 (Ghasempour et al., 2022) –given that the park is protected and not freely accessible everywhere, this number of fires is high. Our former study showed that a savin canopy increases the density and richness of the SSB and the amount of organic matter through litter accumulation (Erfanzadeh et al., 2020). So far there is no study on the effects of savin canopy fire on soil seed banks and soil physicochemical characteristics. Since the species is evergreen, it can be assumed that its crown burns slowly and produces a low temperature during combustion. As a result, the canopy fire may be of low intensity and therefore have no effect on soil parameters and the number of viable seeds in the soil.

The objectives of this study were to assess the effect of burning of savin canopies (and adjacent herbaceous patches) on the density and diversity of the SSB and to compare the intensity of microbial respiration and the amount of organic matter under the savin canopy (and on the herbaceous patch) before and after the fire. In particular, we wanted to test the following hypotheses through comparing the effects of savin canopy and herbaceous patch burning: i) the density and species richness of SSBs beneath the canopy of savin and in herbaceous patches will not significantly change after fire, but ii) soil organic matter and microbial respiration will decrease after burning of both savin canopy and herbaceous plant layer.

2. Materials and methods

2.1. Study area

The study was conducted in the grasslands of the Alborz Mountain chain close to Noor city, Iran (36° 16′ 35″ N – 36° 18′ 19″ N; 51° 49′ 30″ E – 51° 51′ 17″ E). The elevation ranges from 2500 to 3000 m a.s.l. with an average annual rainfall of circa 390 mm and an average annual temperature of 5.5 °C. Savin spreads naturally and characterises most areas together with co-dominant deciduous shrubs like *Onobrychis cornuta* (L.) Desv. and *Acantholimon* spp. In the study area savin grows to an average height of 0.5–1.0 m, its density is 25–40 individuals per ha and its cover 8–15%.

2.2. Site selection and shrub burning

We selected three sampling areas and four randomly chosen individuals of savin in each area, i.e. in total 12 individuals of savin as replications. For each individual a herbaceous control patch was selected as close as possible to the savin to minimise the effects of microclimatic and topographical differences (Fig. 1). The mean area of the herbaceous control patches was 2–4 m^2, each matching the

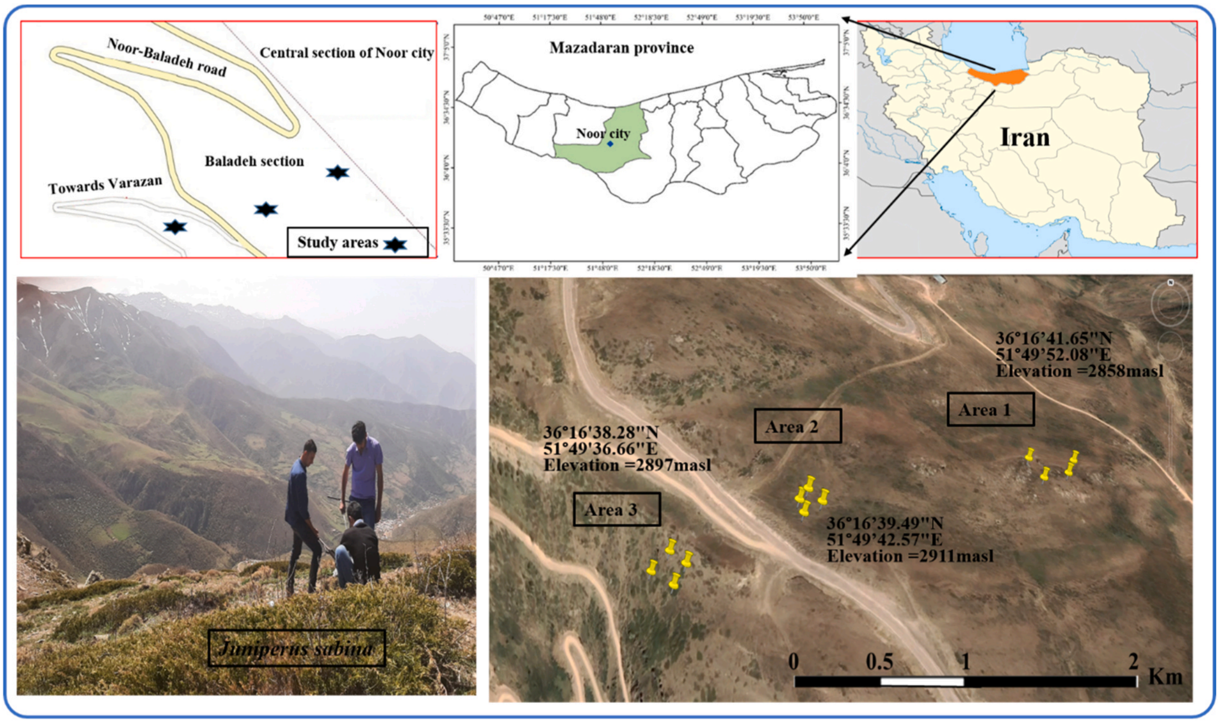

Fig. 1. Geographical location of the study site and the three study areas with twelve individuals of savin and corresponding herbaceous control patches (see text).

area covered by the corresponding savin individual. The control patches were characterised by perennial grasses such as *Festuca ovina* L. and *Bromus tomentellus* Boiss. Herbaceous patches were selected so that the amount of dry material was sufficient for ignition (circa 2 kg/m^2). The amount of dry material was determined before ignition using 0.5 m × 0.5 m sampling plots near to the herbaceous patches.

The distance between the sampling areas was at least 500 m, with at least 50 m distance between two savin individuals nested in each area. Pre- and post-fire soil sampling was performed under the savin canopies and in the adjacent herbaceous control patches in late winter, after the natural stratification of the SSB. Under each savin canopy and in each herbaceous patch, 15 soil cores were collected at random with a 5 cm diameter auger to a depth of 10 cm. The soil samples were divided into two vertical segments of 0–5 cm and 5–10 cm depth. Ten soil cores from each depth were pooled per savin individual and per control patch, giving 48 samples in total for the greenhouse study: (12 savin individuals + 12 control plots) × 2 depths = 48 soil samples. The remaining five soil cores from each depth were also pooled per savin individual and per herbaceous patch, giving another 48 samples for the chemical analysis. In addition, we collected the litter beneath the canopy of each savin individual using a sampling plot of 10 cm × 15 cm (Fig. 2A). The litter was brought to the laboratory and dried using a desiccator. The average dry amount of litter was 5.27 kg/m^2 (79 g per sampling plot).

We used a propane torch to ignite the savin canopies and the herbaceous control patches (Fig. 2B). As an evergreen that recovers only slowly after burning, savin is of conservation interest in the region. Thus, we obtained permission for savin burning (max. 12 individuals) from the corresponding authorities (General Department of Natural Resources and Watershed Management of Nowshahr, Mazandaran Province). An essential aspect of our study was to investigate the effects of fire on the soil seed bank directly after the fire event, before nature recovers or changes the soil characteristics of the burned area. Therefore, the second (post-burning) soil sample was taken immediately after the soil had cooled (Figs. 2C and 2D). Analogous to the pre-fire soil sampling, 48 soil samples were brought to the greenhouse for seed germination experiments and another 48 to the laboratory for chemical analyses. Soil temperatures during burning were not recorded since thermocouples were not available.

2.3. Greenhouse experiments

Each soil sample was evenly distributed at a thickness of 1.2 cm on the surface of a tray (25 cm × 35 cm) filled with a 4 cm layer of sterilised soil. For each sample an individual tray was used. The germination trays were kept under natural light and temperature conditions in an unheated greenhouse and irrigated with tap water when necessary, as described by Hadinezhad et al. (2021). In addition, 10 control trays containing only sterilised soil were randomly placed between the sample trays to detect airborne seed contamination. Germinated seedlings were counted and removed from the trays as soon as they had been identified. Plant species were determined using publications on the flora of Iran (mostly Ghahraman, 1986–, 2014, 32 volumes). After four months, when no further seedlings emerged, the trays were left to dry for two weeks. This caused the samples to crumble, exposing more deeply buried seeds to the light. After the dry period samples were re-irrigated, and the germination continued for another month.

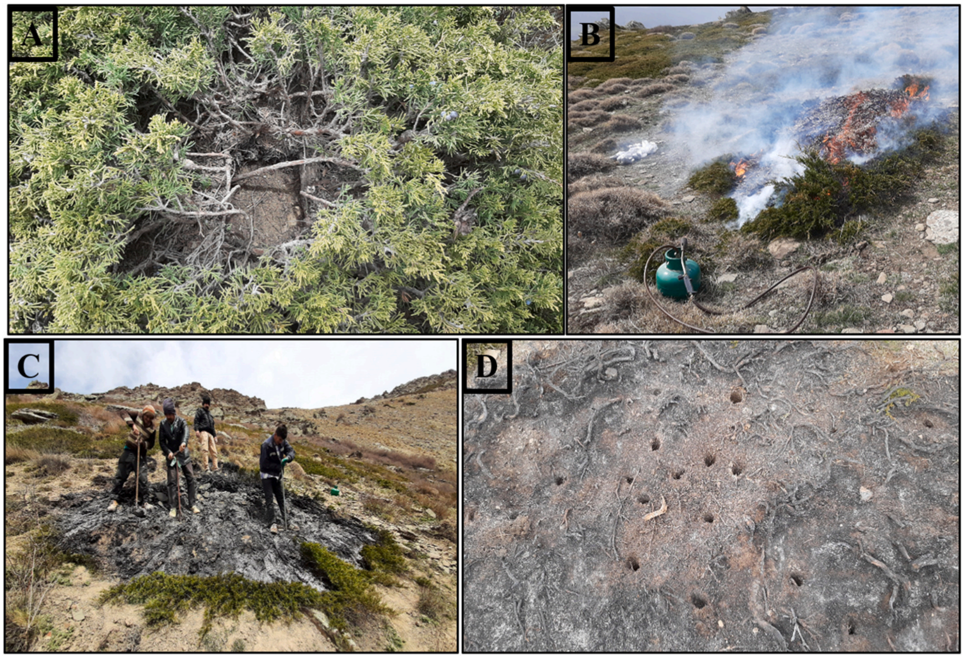

Fig. 2. Litter was collected under the savin canopy using a 10 cm × 15 cm sampling plot (A). A propane torch was used to ignite the savin canopy (B). The second (post-burning) soil sample was taken immediately after the soil had cooled (C and D).

2.4. Laboratory measurements

Soil electrical conductivity (EC) and soil pH were measured using an Orion Ionalyzer Model 125,901 in a 1:2.5 soil/water solution (Sonmez et al., 2008). Soil organic matter was determined by the Walkley-Black method (Sahrawat, 1982).

Following Kamali et al. (2022) for the analyses of basal soil respiration, 50 g of wet soil was transferred to sealed containers. After adding 20 ml of 0.5 M sodium hydroxide solution, the samples were kept separately in containers for 24 h at 25 °C. Finally, the amount of released carbon dioxide was determined titrimetrically using 0.25 normal acid, and the amount of C-CO_2 in mg/kg dry soil was calculated (as described by Anderson, 2015).

To measure the substrate-induced respiration, 100 g of soil was amended with 2 cm^3 of 1% glucose solution in a one-litre plastic container. After adding 10 cm^3 of 0.5 M sodium hydroxide solution, the lid was tightly closed, and the container was incubated at 25 °C for 2 h. Then the titration was performed, the amount of CO_2 determined and the substrate-induced respiration rate calculated (Beare et al., 1990).

2.5. Data analyses

Total SSB density and the abundance of each functional type (annuals (grasses + forbs), perennials (grasses + forbs), forbs (annuals + perennials), grasses (annuals + perennials) and shrubs) in the SSB were used for statistical analyses. The data were checked for homogeneity of variance using Levene's test and normal distribution using the Kolmogorov-Smirnov test. The greenhouse data met normal distribution and could therefore be used without transformation. Total SSB richness (number of species observed under each patch at each soil depth) was calculated for each soil sample. Two-way repeated measures ANOVA models were used to compare total SSB density, total SSB species richness and total abundance of functional groups between the savin and herbaceous patches and between pre- and post-fire with respect to the sampling depths (0–5 cm and 5–10 cm). Total SSB density, total SSB richness and total SSB density of each functional group were used as dependent variables; patch type and sampling depth (two-way) were introduced as fixed factors. Since the interactions between fire and depth and between fire and patch were significant in many cases, we used paired *t* tests to compare SSB characteristics between pre- and post-fire in each depth and in each patch separately. All statistical analyses were done using SPSS 17.0 (SPSS Inc, USA; www.spss.com).

Non-metric dimensional scaling (NMDS) was used to visually analyse the distribution of SSB composition in the space delimited by the pre- and post-fire patches (four groups). Since according to the results of ANOVA and paired *t* test, the fire effects on the SSB density were mostly significant in the upper soil layer (0–5 cm depth), we used the seedling density data of this depth for further NMDS analysis. The NMDS analyses were carried out using the 'vegan' package in R version 3.6.1 (Oksanen et al., 2019).

3. Results

3.1. Soil seed bank composition

In total, 4355 seedlings of 73 species emerged from the soil samples in the greenhouse. The number of seedlings in pre- and post-fire

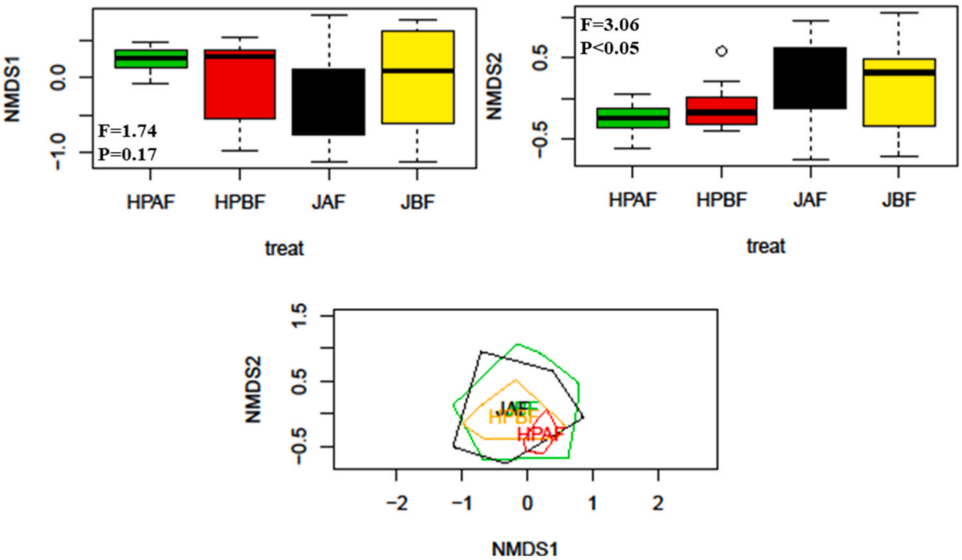

Fig. 3. Non-metric multidimensional scaling (NMDS) of soil seed bank (SSB) composition (0–5 cm) under savin and in herbaceous patches in pre- and post-fire (R2 = 0.94 for non-metric fit, R2 = 0.68 for linear fit and stress = 0.009) (HPBF = herbaceous patch before burning, HPAF = herbaceous patch after burning, JBF = savin before burning and JAF = savin after burning).

soil samples were 2161 and 2194, respectively. The most abundant species in the pre- and post-fire seed banks at 0–5 cm depth under savin were *Stellaria media* (L.) Vill. and *Sisymbrium loeselii* L. with 128 and 52 seedlings, respectively. At 5–10 cm depth it was *S. media* with 28 (pre-fire) and 25 (post-fire) seedlings. In the herbaceous patches the most abundant species was *S. loeselii* (203 and 149 seedlings in pre- and post-fire, respectively) at 0–5 cm depth and *Capsella bursa-pastoris* (L.) Medik (43 and 60 seedlings in pre- and post-fire, respectively) at 5–10 cm depth (Appendix 1).

The studied patch types in pre- and post-fire were not separated along axis 1 or axis 2 of the NMDS (Fig. 3). The NMDS results on the SSBs showed no distinct groups for the two sampling dates (pre- and post-fire) and the two patch types (savin and control). However, the NMDS results on ANOVAs for SSB composition showed significant differences between the four groups (savin and control patches, before and after fire), as can be seen in the ordination histograms ($F = 3.06$, $p < 0.05$).

3.2. Soil seed bank density and richness

The results of repeated measures ANOVA showed that fire, patch, soil depth and their interactions had significant effects on total SSB density and species richness (Table 1). Paired *t* test results showed that at a soil depth of 0–5 cm, fire decreased total SSB density under savin ($t = 3.85$, $p < 0.01$), but had no significant effect on total species richness of the SSB. At 5–10 cm depth fire had no significant effects on total SSB density ($t = 0.18, p = 0.86$) and richness ($t = -0.13, p = 0.89$) beneath savin. In the herbaceous patches fire had no significant effects on total SSB density and species richness, neither at 0–5 cm nor at 5–10 cm depth (Table 2).

3.3. Functional groups in soil seed bank

Repeated measures ANOVAs showed that across both depths, fire, patch type, depth and the interaction between them had significant effects on the SSB density of functional groups in some cases (Table 3). Significant effects of fire on the SSB density of annuals ($F = 6.67, p < 0.05$) and forbs ($F = 4.24, p < 0.05$) were observed. In addition, across both depths the effects of patch and depth on all functional groups (except the effect of depth on shrubs) were significant ($p < 0.05$).

The results of the paired *t* test showed that at 0–5 cm depth under savin, the SSB densities of annuals, perennials and grasses were significantly higher in pre-fire compared to post-fire (Table 4). In the herbaceous patches no significant effects of fire on any functional group were observed at 0–5 cm depth (Table 4). At 5–10 cm depth the fire had no significant effects on the SSB density of any functional group, neither under savin nor in the herbaceous patches (Table 4).

3.4. Soil chemical and biological properties

Variation of soil electrical conductivity between both depths and between pre- and post-fire in both depths was negligible. However, the repeated measures ANOVA results showed that across both depths, fire had a significant effect on the amount of organic matter, basal respiration and substrate-induced respiration ($p < 0.05$; Table 5). At 0–5 cm depth under savin, the paired *t* test showed that fire had a significant effect on pH, basal respiration and substrate-induced respiration. In the herbaceous patches at 0–5 cm depth, the amount of organic matter was significantly higher before fire (3.03% ± 0.06%) than after fire (1.61% ± 0.04%), whereas fire had no significant effect on the other soil properties (Table 6). At 5–10 cm depth under savin, soil pH was significantly decreased by fire, whereas fire had no significant effects on organic matter, basal and substrate-induced respirations. In the herbaceous patches at 5–10 cm depth, the amount of organic matter and basal respiration was higher before burning (3.13% ± 0.07% and 17.41% ± 3.41%, respectively) than post-fire (2.18% ± 0.03% and 10.83% ± 2.01%, respectively) (Table 6).

Table 1
Repeated measures ANOVA results of total soil seed bank density and species richness through analyses of data across the two soil depths and for each depth separately.

		Density				Richness			
	Factor	*df*	Mean square	*F*	*p*	*df*	Mean square	*F*	*p*
Total	Fire	1	1944.00	8.54	**< 0.01**	1	4.16	0.39	0.532
	Patch	1	18872.04	27.53	**< 0.01**	1	66.66	1.98	0.166
	Soil depth	1	52547.04	76.68	**< 0.01**	1	1305.37	38.79	**< 0.01**
	Fire×Patch	1	2.04	0.00	0.925	1	73.50	6.99	**< 0.05**
	Fire×Depth	1	1890.37	8.30	**< 0.01**	1	3.37	0.32	0.574
	Patch×Depth	1	9600.00	14.00	**< 0.01**	1	40.04	1.19	0.281
	Fire×Patch×Depth	1	6.00	0.02	0.872	1	30.37	2.88	0.096
0–5 cm	Fire	1	3834.18	8.70	**< 0.01**	1	0.02	0.00	0.970
	Patch	1	27696.02	21.43	**< 0.01**	1	105.02	1.81	0.192
	Fire× Patch	1	7.52	0.017	0.897	1	99.18	6.70	**< 0.05**
5–10 cm	Fire	1	0.18	0.01	0.911	1	7.52	1.20	0.284
	Patch	1	776.02	9.92	**< 0.01**	1	1.68	0.17	0.677
	Fire× Patch	1	0.52	0.03	0.852	1	4.68	0.75	0.395

Table 2
Results of the paired *t* test used to compare total soil seed bank density and species richness of different vegetation types (savin and herbaceous patches) between pre- and post-fire.

	Patch	Depth	Burning	Mean	*SE*	*df*	*t*	*p*
Total soil seed bank density	*Juniperus sabina*	0–5	pre	43.58	7.75	11	3.85	**< 0.01**
			post	26.5	5.43			
		5–10	pre	8.42	1.63	11	0.18	0.86
			post	8.08	1.27			
	Herbaceous patch	0–5	pre	92.42	12.78	11	1.65	0.13
			post	73.75	5.98			
		5–10	pre	16.25	2.72	11	− 0.07	0.94
			post	16.33	1.93			
Total soil seed bank richness	*Juniperus sabina*	0–5	pre	12.5	2.20	11	1.70	0.12
			post	9.66	1.75			
		5–10	pre	4.91	1.10	11	− 0.13	0.89
			post	5.08	0.80			
	Herbaceous patch	0–5	pre	12.58	1.70	11	− 1.97	0.07
			post	15.50	1.12			
		5–10	pre	4.66	0.60	11	− 2.02	0.06
			post	6.08	0.62			

4. Discussion

4.1. Fire effects on soil seed bank

Our study demonstrated that generally, the immediate effect of savin canopy fire on the underlying soil seed bank and biological and chemical parameters was significantly negative. Although the results of the NMDS showed little difference of SSB composition between pre- and post-fire, the number of seeds in the soil under the canopies was decreased by the fire in both savin and herbaceous patches. This depletion was more pronounced under savin. No such strong effect of fire was detected for the density of the SSBs in the herbaceous control patches, particularly at 0–5 cm depth. These results did not confirm our first hypothesis. One likely reason for the difference between savin and herbaceous patches is that higher amounts of accumulated litter under savin provide a higher fuel load for a more intense fire in comparison with the herbaceous patch. Apparently, litter accumulation and consumption of greater quantities of fuel on the soil surface affected the survival of seeds in the post-fire SSB (Tangney et al., 2020). Higher litter input and a lower litter decomposition rate led to a fuel accumulation under savin. It was shown that litter formed by juniper leaves decomposes relatively slowly (Bates et al., 2007). This is generally attributed to the high amount of lignin and low N concentrations in needle litter, but may more precisely be the result of low labile content and hence low mineralisation of organic matter in the decomposition process (Prescott et al., 2017). Besides litter accumulation by savin itself, the crown of the shrub can act as a trap for litter produced by plants in the surroundings (Yan et al., 2016; Erfanzadeh et al., 2021). Our study showed that the amount of dry litter under savin was circa 2.5 times higher than in adjacent herbaceous patches. The larger fuel supply is likely to produce higher combustion temperatures, thus killing more seeds (Tangney et al., 2020). In accordance with our results, Auld and Denham (2006) reported that in open woodlands with a dense shrub layer, the SSB contained only few viable seeds in areas burned by fire. They stated that soil temperatures during fires were strongly dependent on the amount of available fuel. Similarly, in a semi-arid shrubland a significant decrease of the SSB density due to intense fire of accumulated litter was reported (Lipoma et al., 2018). In contrast, the soil sampling by de Andrade and Miranda (2014) in a woody savanna immediately after a fire showed a non-significant difference between pre- and post-fire SSB density. They demonstrated that after the fire the viable seed density and species richness may decrease with the onset of the rain season coinciding with germination in the field. In addition to the heat produced by the combustion of accumulated litter, some studies indicated that in regions with tall shrubs and trees, shallow soils are warmer under the canopy of shrubs than in open areas (Kropp et al., 2021). It can therefore be assumed that the threshold temperatures for killing seeds are reached earlier under shrubs than in herbaceous patches. Moreover, herbaceous fires are often rapidly moving with the wind (personal observation) so that soil heating may not reach a harmful level and therefore damage is much less than during crown, surface or smouldering fires under shrubs.

S. media was the most abundant species in the SSB under savin before burning. After the fire the SSB density of this species was significantly decreased. The decrease in the seed density of this species alone could be responsible for the decrease of the SSB density of the functional group 'annuals' by fire under savin. This species produces a large number of small seeds, which can remain viable in soil for a long time (Bitarafan and Andreasen, 2020). It can be assumed that the heat of the fire mainly affected seeds in the upper soil layer (at 0–5 cm depth), which is where most of the seeds of the annual *S. media* are deposited. Hence the fire was able to deplete large amounts of *S. media* seeds. However, the seed numbers of some other annuals such as *Medicago minima* (L.) Bartal. increased slightly by fire or showed no significant changes after shrub (or herbaceous) burning. Exposure to temperatures between 80 and 100 °C has been shown to break the seed dormancy of several annuals such as legumes in north-eastern Australia, but temperatures above 100–120 °C are lethal to seeds of these species (Williams et al., 2003; Gresta et al., 2011; Dairel and Fidelis, 2020). Pausas and Lamont (2022) compiled data from a wide range of fire-related germination experiments for species in different ecosystems across the globe and reported that studies on the effects of fire on the soil seed bank under shrub crown consistently show an overall increase in annual seedling density and species richness.

Table 3
Repeated measures ANOVA results of soil seed bank density of functional groups through analyses of data across the two soil depths and for each depth separately.

Functional group	Depth	Factor	*df*	Mean square	*F*	*p*
Annuals	Total	Fire	1	975.37	6.67	**< 0.05**
		Patch	1	8177.04	18.40	**< 0.01**
		Depth	1	16907.04	38.05	**< 0.01**
		Fire×Patch	1	112.66	0.77	0.39
		Fire×Depth	1	1176.00	8.04	**< 0.01**
		Patch×Depth	1	4537.50	10.21	**< 0.01**
		Fire×Patch×Depth	1	234.37	1.60	0.21
	0–5 cm	Fire	1	2146.68	7.74	**< 0.05**
		Patch	1	12448.52	14.52	**< 0.01**
		Fire× Patch	1	336.02	1.21	0.28
	5–10 cm	Fire	1	4.68	0.30	0.58
		Patch	1	266.02	8.42	**< 0.01**
		Fire×Patch	1	11.02	0.72	0.40
Perennials	Total	Fire	1	165.37	1.80	0.19
		Patch	1	2204.16	13.71	**< 0.01**
		Depth	1	9841.50	61.27	**< 0.01**
		Fire×Patch	1	84.37	0.92	0.34
		Fire×Depth	1	84.37	0.92	0.34
		Patch×Depth	1	937.50	5.83	**< 0.05**
		Fire×Patch×Depth	1	91.48	1.80	0.19
	0–5 cm	Fire	1	243.00	1.44	0.24
		Patch	1	3008.33	10.83	**< 0.01**
		Fire× Patch	1	243.00	1.44	0.24
	5–10 cm	Fire	1	6.75	0.44	0.51
		Patch	1	133.33	3.03	0.09
		Fire×Patch	1	6.75	0.44	0.51
Forbs	Total	Fire	1	962.66	4.24	**< 0.05**
		Patch	1	13680.37	24.68	**< 0.01**
		Depth	1	37604.16	67.86	**< 0.01**
		Fire×Patch	1	45.37	0.20	0.66
		Fire×Depth	1	1066.66	4.70	**< 0.05**
		Patch×Depth	1	7455.37	13.45	**< 0.01**
		Fire×Patch×Depth	1	92.04	0.40	0.58
	0–5 cm	Fire	1	2028.00	4.66	**< 0.05**
		Patch	1	20667.00	19.37	**< 0.01**
		Fire× Patch	1	133.33	0.30	0.58
	5–10 cm	Fire	1	1.33	0.07	0.79
		Patch	1	468.75	11.24	**< 0.01**
		Fire×Patch	1	4.08	0.21	0.64
Grasses	Total	Fire	1	137.76	3.90	0.05
		Patch	1	276.76	10.42	**< 0.01**
		Depth	1	810.84	30.53	**< 0.01**
		Fire×Patch	1	17.51	0.49	0.48
		Fire×Depth	1	94.01	2.66	0.11
		Patch×Depth	1	86.26	3.24	0.08
		Fire×Patch×Depth	1	33.84	0.96	0.33
	0–5 cm	Fire	1	229.68	3.78	0.06
		Patch	1	336.02	8.07	**< 0.01**
		Fire× Patch	1	50.02	0.82	0.37
	5–10 cm	Fire	1	2.08	0.21	0.65
		Patch	1	27.00	2.34	0.14
		Fire×Patch	1	1.33	0.13	0.71
Shrubs	Total	Fire	1	1.76	0.24	0.62
		Patch	1	14.26	1.85	0.18
		Depth	1	46.76	6.07	**< 0.05**
		Fire×Patch	1	1.26	0.17	0.67
		Fire×Depth	1	1.26	0.17	0.67
		Patch×Depth	1	5.51	0.71	0.40
		Fire×Patch×Depth	1	1.76	0.24	0.62
	0–5 cm	Fire	1	3.00	0.22	0.64
		Patch	1	18.75	1.33	0.26
		Fire× Patch	1	3.00	0.22	0.64
	5–10 cm	Fire	1	0.02	0.02	0.87
		Patch	1	1.02	0.73	0.40
		Fire×Patch	1	0.02	0.02	0.87

Table 4
Results of the paired *t* test used to compare functional groups of soil seed bank density of different vegetation types (savin and herbaceous patches) between pre- and post-fire.

Functional group	Patch	Depth	Burning	Mean	*SE*	*df*	*t*	*p*
Annuals	*Juniperus sabina*	0–5	pre	19.91	6.74	11	2.12	**< 0.05**
			post	11.83	3.23			
		5–10	pre	3.25	1.10	11	0.24	0.81
			post	2.91	0.93			
	Herbaceous patch	0–5	pre	57.41	10.36	11	2.01	0.07
			post	48.75	5.06			
		5–10	pre	7.00	1.66	11	− 0.87	0.39
			post	8.58	1.71			
Perennials	*Juniperus sabina*	0–5	pre	23.66	4.51	11	2.87	**< 0.05**
			post	14.66	3.88			
		5–10	pre	5.16	1.13	11	0.00	1.00
			post	5.16	1.09			
	Herbaceous patch	0–5	pre	35.00	5.56	11	0.00	1.00
			post	35.00	2.79			
		5–10	pre	9.25	2.39	11	0.82	0.43
			post	9.25	1.27			
Forbs	*Juniperus sabina*	0–5	pre	32.75	7.04	11	2.13	0.06
			post	23.08	4.98			
		5–10	pre	6.08	1.13	11	0.15	0.88
			post	5.83	1.05			
	Herbaceous patch	0–5	pre	77.58	11.15	11	1.46	0.17
			post	61.25	7.17			
		5–10	pre	11.75	1.90	11	− 0.48	0.64
			post	12.66	2.00			
Grasses	*Juniperus sabina*	0–5	pre	9.08	2.32	11	2.78	**< 0.05**
			post	2.66	0.87			
		5–10	pre	2.00	0.67	11	0.13	0.89
			post	1.91	0.76			
	Herbaceous patch	0–5	pre	12.33	2.86	11	0.60	0.56
			post	10.00	1.63			
		5–10	pre	3.83	1.34	11	0.44	0.67
			post	3.08	0.83			
Shrubs	*Juniperus sabina*	0–5	pre	1.75	0.57	11	1.86	0.09
			post	0.75	0.30			
		5–10	pre	0.33	0.14	11	0.00	1.00
			post	0.33	0.14			
	Herbaceous patch	0–5	pre	2.50	1.46	11	0.00	1.00
			post	2.50	1.42			
		5–10	pre	0.66	0.51	11	0.18	0.86
			post	0.58	0.22			

Surprisingly, in our study the seed germination of most species of the 'shrub' functional group showed a negative reaction to the fire (e.g. *Acantholimon erinaceum* (Jaub. & Spach) Lincz and *Artemisia chamaemelifolia* Vill.). The only shrub whose SSB density increased slightly after burning was *Astragalus aegebromus* L. Seedlings of this species were absent in the pre-fire samples in the greenhouse, while they occurred in the post-fire samples from both savin and herbaceous patches. The fact that some legumes showed a positive reaction to fire may be explained by their dehiscent fruits, whose germination is facilitated by heat (Risberg, 2015). Ruprecht et al. (2013) identified several species, some of which belong to the Fabaceae family, to have heat-stimulated germination. In our study 10 and 9 species (mostly perennials) were absent under savin canopy in the pre-fire samples at 0–5 cm and 5–10 cm depth, respectively, but appeared in the greenhouse in the post-fire samples. However, in view of the low numbers of individuals (mostly only one seedling) it can be assumed that these species occurred incidentally during the post-fire sampling period: The number of seedlings was negligible and very unlikely a result of the fire. However, a few species absent in the pre-fire samples showed a high abundance in the post-fire samples, e.g. *Mentha longifolia* (L.) Huds. and *Polygonum aviculare* L. It appears that the seeds of these species are tolerant to fire and that heat may even favour their germination.

The overall high depletion of the SSB under savin by burning indicates that successful post-fire recovery may not rely on the buried seeds, but on spatial seed dispersal. The open gaps created through savin burning can be re-colonised via plant seeds or by vegetative plant growth from outside. Surprisingly, savin itself was absent in the SSB both before and after burning (only one seed germinated in the greenhouse in the pre-fire samples). Probably this species is not able to produce viable seeds, its seeds remain dormant even after a fire, or the seeds decayed in the greenhouse processing (Thompson et al., 1997).

Our results show that for most plant functional groups, the decrease in total SSB density following fire was more pronounced at the 0–5 cm depth of soil than at the 5–10 cm depth. Higher intensity and longer impact of fire on shallow soil layers compared to deeper ones (Girona-Garcia et al., 2015) could lead to higher levels of seed depletion (Auld and Denham, 2006). Indeed, the highest SSB depletion of our study occurred in the upper soil layer, presumably due to higher temperatures in this layer (Tangney et al., 2020; Ghasempour et al., 2022).

Table 5
Repeated measures results of soil chemical and biological properties through analyses of data across the two soil depths and for each depth separately.

Soil property	Depth	Factor	*df*	Mean square	*F*	*p*	Soil property	Mean square	*F*	*p*
pH	Total	Fire	1	0.38	1.53	0.22	Organic matter	14.10	17.50	**< 0.01**
		Patch	1	2.66	13.39	**< 0.01**		0.07	0.08	0.78
		Depth	1	0.43	2.18	0.14		0.41	0.48	0.49
		Fire×Patch	1	1.74	6.97	**< 0.05**		4.13	5.13	**< 0.05**
		Fire×Depth	1	0.03	0.01	0.91		0.69	0.86	0.35
		Patch×Depth	1	0.14	0.69	0.41		0.95	1.11	0.29
		Fire×Patch×Depth	1	0.13	0.51	0.48		0.09	0.12	0.73
	0–5 cm	Fire	1	0.23	1.28	0.29		281.13	512.03	**< 0.01**
		Patch	1	0.79	4.64	**< 0.05**		0.88	1.29	0.27
		Fire×Patch	1	1.40	7.92	**< 0.01**		1.51	2.74	0.11
	5–10 cm	Fire	1	0.16	0.49	0.49		4.26	5.45	**< 0.05**
		Patch	1	2.01	8.86	**< 0.01**		0.76	0.98	0.33
		Fire×Patch	1	0.46	1.44	0.24		1.48	1.90	0.18
Basal soil respiration	Total	Fire	1	2016.67	13.12	**< 0.01**	Substrate-induced respiration	0.16	8.11	**< 0.01**
		Patch	1	7038.37	34.10	**< 0.01**		0.93	35.42	**< 0.01**
		Depth	1	2926.04	14.17	**< 0.01**		0.57	21.68	**< 0.01**
		Fire×Patch	1	1305.37	8.49	**< 0.01**		0.24	12.40	**< 0.01**
		Fire×Depth	1	22.04	0.14	0.71		0.01	0.40	0.53
		Patch×Depth	1	60.17	0.29	0.59		0.02	0.18	0.67
		Fire×Patch×Depth	1	793.50	5.16	**< 0.05**		0.06	2.95	0.09
	0–5 cm	Fire	1	230.19	6.09	**< 0.05**		0.12	5.12	**< 0.05**
		Patch	1	4200.02	24.02	**< 0.01**		0.40	22.22	**< 0.01**
		Fire×Patch	1	2067.19	10.22	**< 0.01**		0.27	11.57	**< 0.01**
	5–10 cm	Fire	1	808.52	7.68	**< 0.05**		0.05	3.01	0.09
		Patch	1	2898.52	12.18	**< 0.01**		0.54	15.48	**< 0.01**
		Fire×Patch	1	31.69	0.30	0.59		0.03	1.99	0.17

Table 6
The results of the paired *t* test used to compare soil chemical and biological properties of different patch types (savin and herbaceous patches) between pre- and post-fire.

Soil property	Patch	Depth	Burning	Mean	*SE*	*df*	*t*	*p*
pH	*Juniperus sabina*	0–5	pre	6.73	0.12	11	− 4.03	**< 0.01**
			post	7.21	0.09			
		5–10	pre	7.02	0.08	11	− 2.28	0.06
			post	7.33	0.10			
	Herbaceous patch	0–5	pre	6.81	0.14	11	0.96	0.35
			post	6.61	0.11			
		5–10	pre	6.81	0.13	11	0.28	0.79
			post	6.73	0.24			
Organic matter	*Juniperus sabina*	0–5	pre	2.70	0.22	11	1.19	0.29
			post	2.24	0.26			
		5–10	pre	2.52	0.28	11	0.62	0.54
			post	2.28	0.24			
	Herbaceous patch	0–5	pre	3.03	0.27	11	3.94	**< 0.01**
			post	1.61	0.31			
		5–10	pre	3.13	0.33	11	2.92	**< 0.05**
			post	2.18	0.11			
Basal soil respiration	*Juniperus sabina*	0–5	pre	17.86	5.15	11	3.18	**< 0.01**
			post	14.11	4.07			
		5–10	pre	34.58	4.97	11	1.89	0.08
			post	24.75	4.85			
	Herbaceous patch	0–5	pre	22.08	2.19	11	− 0.80	0.44
			post	25.08	3.84			
		5–10	pre	17.41	2.47	11	2.32	**< 0.05**
			post	10.83	1.65			
Substrate-induced respiration	*Juniperus sabina*	0–5	pre	0.65	0.05	11	3.53	**< 0.01**
			post	0.35	0.04			
		5–10	pre	0.39	0.06	11	1.84	0.09
			post	0.28	0.05			
	Herbaceous patch	0–5	pre	0.27	0.02	11	− 0.96	0.36
			post	0.32	0.04			
		5–10	pre	0.13	0.03	11	0.31	0.76
			post	0.12	0.02			

4.2. Fire effects on biological and chemical soil parameters

Burning of the savin canopy decreased basal and substrate-induced soil respiration in the upper soil layer (0–5 cm depth). This decrease was not detected in any of the soil layers in the herbaceous patches. Therefore, it might be assumed that burning the savin canopy resulted in a higher fire intensity than burning the herbaceous patches. Fire has been proven to cause significant changes in soil respiration in many studies. For example, it was shown that high temperatures during an intensive fire can reduce soil microbial biomass and thus soil microbial activity directly after a fire (Dooley and Treseder, 2012; Ludwig et al., 2018; Lucas-Borja et al., 2019; Barreiro and Díaz-Raviña, 2021). A decrease in enzyme activities one (Armas-Herrera et al., 2018), three (Borgogni et al., 2019) and eighteen days (Fairbanks et al., 2020) after fire events was also found. Pillay et al. (2023) studied the effect of environmental conditions on the nitrogen fixation rate of woody plants in savannas. They stated that fire can decrease soil microbial respiration through removing biomass. In addition, different impacts on different microbial communities were reported in some studies. For instance, Rai et al. (2023) found that bacterial and fungal diversity and community composition at the phylum level showed no short-term changes, whereas at the order level, bacterial Desulfurellales increased and fungal Eurotiales and Pleosporales decreased two days after fire.

Although some research indicated that fire could promote soil microbial activities in the long run due to increasing soil pH and nutrient availability (Barreiro et al., 2016; Stirling et al., 2019), we found in our study that fire increased pH under savin, but decreased soil respiration. Some studies found that an increase in the availability of soil ammonium and nitrate (parameters we did not measure in our study) through the burning of plant tissue can promote microbial activity and respiration (Day et al., 2006), and others showed that soil respiration did not differ between burned and unburned areas (e.g. Hedo et al., 2014). These inconsistencies with our results might be due to differences between the time of soil sampling after burning: We sampled the soil immediately after vegetation burning, whereas in the other studies the time span between fire and sampling was longer.

Our results showed that through burning SOM was decreased (albeit not significantly) under savin by 17% and 9.5% at 0–5 cm and 5–10 cm depth, respectively. In the herbaceous patches SOM was significantly decreased by fire: by 46% at 0–5 cm depth and by 30.4% at 5–10 cm depth. In many studies fire effects on SOM were investigated over a relatively long period, in which post fire samplings were done from one to many years after burning (e.g., Köster et al., 2014; Parro et al., 2019). In most of these studies, the SOM content was decreased by fire. Disturbance by fire is often considered to result in SOM losses because fires combust plant biomass and organic soil layers and promote erosion and leaching, subsequently reducing inputs to and stimulating losses from soils, which can persist for several years after a fire (Pellegrini et al., 2022). It has been shown that SOM content in recently burned areas, where fire occurred $<$ 10 years ago, is lower compared to unburned areas or areas where fire has occurred more than 10 years ago (e.g. Köster et al., 2014 in boreal forests; Parro et al., 2019 and Orumaa et al., 2022 in hemi-boreal forests; Salim et al., 2022 in high altitude grasslands). Parro et al. (2019) stated that twenty years may be an insufficient time for carbon dynamics to fully recover after a fire on low productivity sandy sites. However, a few studies on the immediate effects of fire also showed a loss of SOM by burning (e.g. Rai et al., 2023 in a rangeland ecosystem two days after burning). This can be a result of the organic soil layer being burned by fire (see also Hrelja et al., 2020). Certini (2005), Armas-Herrera et al. (2016) and Zufiaurre-Galarza et al. (2016) reported that the quantity of organic matter in soil was decreased immediately after a fire due to ignition and burning of the soil organic layer. Conversely, in a few studies SOM was found to be increased after fire. This increase mostly occurred immediately after low-intensity fires. Pereira et al. (2013) reported that the SOM content was significantly higher in a burned grassland plot as compared to an unburned plot three days to two months after the fire. Xifré-Salvadó et al. (2021) demonstrated that in a *Pinus halepensis* forest a fire with low intensity did not have a significant negative short-term impact on the soil.

The varied results of our study for the post-fire pH are supported by other studies, in which immediate changes of soil pH after burning of evergreen woody plants are reported (e.g. González-Pérez et al., 2000 in Mediterranean forests; Bridges et al., 2019 in temperate forests and Hrelja et al., 2022 in Mediterranean shrublands). We found the pH of the topsoil layer to be significantly changed from 6.73 (pre-fire) to 7.23 (post-fire) under savin, whereas in the herbaceous patch no significant change was observed, neither in the topsoil nor in the deeper soil layer. Probably, ash from the combustion of savin and litter caused an increase in pH. On the herbaceous patches lesser ash was produced in the fire, and thus the change in pH was negligible. The increase of pH under savin was to be expected as the carbonates and oxides produced from combustion are highly alkaline. This is supported by other studies, which also found that topsoil pH (including the ash layer) under needle evergreen plants increased immediately after the burning (Ulery et al., 1993; Bridges et al., 2019). Therefore, it is likely that ash and its components leached into the ground by rain turns the soil from slightly acidic to slightly alkaline under burned savin. The increase in pH may limit the number of species contributing to the restoration of burned open gaps through the remaining SSB to those that are tolerant to alkaline soil.

5. Conclusions

The main aim of this study was to measure and analyse the immediate effects of fire on soil under the procumbent canopy of evergreen savin. This was done by burning a representative but small number of savin individuals, which allowed shrub fire effects on soil to be measured without extensive damage. In a mountainous grassland that is one of the world's largest habitats of *J. sabina*, the experimental fire produced significant changes to the soil seed bank, organic matter and biological properties within the small and clearly limited sample patches where it was ignited. Increased changes were most obvious in the topsoil layer, in which the soil seed bank was strongly depleted and the soil lost a large amount of organic matter and probably microbes. Therefore, it should be considered in site management that the restoration of gaps created by fire cannot rely on a viable soil seed bank. In addition, the recovery of burned open gaps through the soil seed bank might be hampered for a relatively long time by the alkalisation of the soil and the decrease in soil quality caused by fire.

Declaration of Competing Interest

The authors have no relevant financial or non-financial interests to disclose.

Data Availability

Data will be made available on request.

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Appendix 1. Species composition and mean density of the soil seed bank (SSB) of each species per m^2 in pre- and post-fire situation at 0–5 cm and 5–10 cm depth under *Juniperus sabina* (savin) and in the herbaceous patch. P = Perennial, A = Annual, F = Forb, G = Grass, S = Shrub

Species name	Family	Life cycle	Life form	Savin				Herbaceous patch			
				Before fire		After fire		Before fire		After fire	
				0–5 cm	5–10 cm	0–5 cm	5–10 cm	0–5 cm	5–10 cm	0–5 cm	5–10 cm
Achantolimon erinaceum	Plumbaginaceae	P	S	4.25	0.00	0.00	0.00	12.74	0.00	4.25	0.00
Achillea millefolia	Asteraceae	P	F	63.69	12.7	8.49	8.49	8.49	4.25	4.25	4.25
Achillea wilhelmsii	Asteraceae	P	F	16.98	0.00	4.25	8.49	0.00	0.00	4.25	4.25
Adiantum capillus-veneris	Pteridaceae	P	F	55.20	12.74	8.49	4.25	42.46	12.74	29.72	8.49
Adonis aestivalis	Ranunculaceae	A	F	8.49	4.25	4.25	8.49	0.00	0.00	0.00	0.00
Aegilops tauschii	Poaceae	A	G	8.49	4.25	4.25	4.25	271.73	4.25	110.39	12.74
Alchemilla hyrcana	Rosaceae	P	F	8.49	0.00	8.49	8.49	0.00	0.00	0.00	0.00
Allium atraviolacum	Amaryllidaceae	P	G	67.93	12.74	8.49	12.74	4.25	80.67	8.49	84.92
Allysum minus	Brassicaceae	A	F	0.00	0.00	12.74	0.00	0.00	0.00	0.00	0.00
Alopecurus textilis	Poaceae	P	G	16.98	0.00	8.49	0.00	233.52	25.48	229.28	29.72
Artemisia annua	Asteraceae	A	F	12.74	0.00	16.98	4.25	0.00	0.00	0.00	0.00
Artemisia chamaemelifolia	Asteraceae	P	S	29.72	0.00	8.49	0.00	16.98	25.48	4.25	21.23
Asperula odorata	Rubiaceae	P	F	55.20	29.72	67.93	12.74	16.98	12.74	42.46	12.74
Astragalus aegebromus	Fabaceae	P	S	0.00	4.25	8.49	4.25	0.00	0.00	4.25	0.00
Brachypodium pinnatum	Poaceae	P	G	72.18	4.25	8.49	0.00	0.00	33.97	0.00	0.00
Bromus tomentellus	Poaceae	P	G	25.48	50.95	0.00	50.95	21.23	12.74	46.70	25.48
Capsella bursa-pastoris	Brassicaceae	A	F	33.97	4.25	4.25	0.00	645.37	182.57	573.19	254.75
Circium vulgare	Asteracea	P	F	46.70	0.00	80.67	0.00	16.98	33.97	16.98	33.97
Cynodon doctylon	Poaceae	P	G	16.98	0.00	21.23	0.00	0.00	0.00	0.00	0.00
Cynoglossum creticum	Boraginaceae	P	F	25.48	0.00	21.23	4.25	16.98	0.00	42.46	8.49
Cynoglossum disticum	Boraginaceae	A	F	4.25	0.00	16.98	0.00	38.21	12.74	42.46	21.23
Dianthus orientalis	Caryophyllaceae	P	F	0.00	0.00	8.49	0.00	8.49	4.25	21.23	4.25
Dianthus sp.	Caryophyllaceae	P	F	135.87	8.49	21.23	4.25	84.92	4.25	127.38	8.49
Ephorbia helisocopia	Euphorbiaceae	A	F	8.49	0.00	25.48	0.00	0.00	4.25	0.00	0.00
Erigeron canadensis	Asteracea	A	F	25.48	8.49	8.49	4.25	0.00	0.00	0.00	0.00
Erodium graminacea	Geraniaceae	A	F	42.46	0.00	38.21	0.00	246.26	93.41	208.05	140.11
Eryngium bungei	Apiaceae	P	S	38.21	0.00	8.49	0.00	0.00	0.00	0.00	0.00
Ferula ovina	Poaceae	P	F	4.25	0.00	63.69	0.00	46.70	59.44	46.70	59.44
Festuca ovina	Poaceae	P	G	148.60	12.74	29.72	16.98	55.20	29.72	46.70	4.25
Galium verum	Rubiaceae	P	F	38.21	0.00	25.48	8.49	339.67	33.97	123.13	42.46
Geranium collinum	Geraniaceae	P	F	16.98	4.25	0.00	8.49	0.00	4.25	0.00	0.00
Geranium tuberosum	Geraniaceae	P	F	42.46	12.74	16.98	4.25	63.69	0.00	72.18	4.25
Hypericum hepsofilum	Hypericaceae	P	F	0.00	4.25	4.25	0.00	80.67	0.00	72.18	8.49
Juniperus sabina	Cupressaceae	P	S	4.25	4.25	0.00	0.00	0.00	0.00	0.00	0.00
Lamium album	Lamiaceae	P	F	16.98	4.25	0.00	4.25	21.23	0.00	29.72	4.25
Lycopus eurpou	Lamiaceae	P	F	0.00	0.00	0.00	0.00	55.20	0.00	89.16	0.00
Malva sp.	Malvaceae	A	F	0.00	4.25	0.00	0.00	0.00	0.00	0.00	0.00

(*continued on next page*)

(*continued*)

Species name	Family	Life cycle	Life form	Savin				Herbaceous patch			
				Before fire		After fire		Before fire		After fire	
				0–5 cm	5–10 cm	0–5 cm	5–10 cm	0–5 cm	5–10 cm	0–5 cm	5–10 cm
Malva sylvestris	Malvaceae	A	F	12.74	0.00	25.48	4.25	4.25	0.00	0.00	0.00
Medicago minima	Fabaceae	A	F	38.21	8.49	46.70	8.49	93.41	0.00	110.39	8.49
Mentha longifolia	Lamiaceae	P	F	0.00	0.00	25.48	4.25	4.25	0.00	0.00	0.00
Nonnea lutea	Boraginaceae	P	F	0.00	0.00	0.00	0.00	4.25	0.00	4.25	0.00
Phleum paniculatum	Poaceae	P	G	0.00	8.49	8.49	0.00	0.00	0.00	0.00	0.00
Phlomis olivieri	Lamiaceae	P	F	8.49	4.25	0.00	0.00	0.00	0.00	0.00	0.00
Plantago atrata	Plantaginaceae	P	F	0.00	0.00	0.00	0.00	21.23	0.00	46.70	0.00
Plantago major	Plantaginaceae	A	F	12.74	8.49	4.25	4.25	4.25	0.00	0.00	0.00
Poa annua	Poaceae	A	G	0.00	0.00	0.00	0.00	0.00	8.49	0.00	0.00
Poa bulbosa	Poaceae	P	G	33.97	4.25	0.00	4.25	0.00	0.00	25.48	0.00
Poa mazandrana	Poaceae	P	G	0.00	0.00	0.00	0.00	12.74	0.00	0.00	0.00
Poa pratensis	Poaceae	P	G	8.49	4.25	16.98	8.49	0.00	0.00	0.00	0.00
Polygonum aviculare	Polygonaceae	A	F	0.00	0.00	50.95	4.25	0.00	0.00	0.00	0.00
Polygonum fugax	Polygonaceae	P	F	0.00	0.00	4.25	4.25	21.23	0.00	38.21	0.00
Potentilla argentea	Rosaceae	P	F	0.00	4.25	0.00	4.25	4.25	0.00	0.00	0.00
Potentilla reptanse	Rosaceae	P	F	0.00	0.00	4.25	0.00	8.49	0.00	0.00	0.00
Poterium sanguisorba	Rosaceae	P	F	8.49	8.49	38.21	16.98	38.21	16.98	0.00	0.00
Prunella vulgaris	Lamiaceae	P	F	0.00	0.00	4.25	0.00	0.00	0.00	0.00	0.00
Rumex chalepensis	Polygonaceae	P	F	0.00	0.00	8.49	0.00	0.00	0.00	0.00	0.00
Sedum album	Crassulaceae	P	F	4.25	0.00	12.74	4.25	199.55	0.00	186.82	0.00
Senecio vernalis	Asteraceae	A	F	0.00	0.00	4.25	0.00	4.25	0.00	4.25	0.00
Setaria viridis	Poaceae	A	G	50.95	0.00	8.49	0.00	29.72	0.00	0.00	0.00
Sisymbrium loeselii	Brassicaceae	A	F	212.29	4.25	220.78	0.00	861.90	0.00	632.63	0.00
Stachys lavandulifolia	Lamiaceae	P	F	38.21	21.23	72.18	29.72	50.95	42.46	0.00	4.25
Stellaria media	Caryophyllaceae	A	F	543.47	118.88	110.39	106.15	726.04	50.95	292.96	0.00
Taraxacum brivestrum	Asteraceae	P	F	12.74	0.00	25.48	4.25	29.72	0.00	46.70	0.00
Taraxacum montanum	Asteraceae	P	F	12.74	0.00	25.48	0.00	0.00	12.74	0.00	8.49
Taraxacum officinalis	Asteraceae	P	F	29.72	12.74	4.25	0.00	0.00	0.00	4.25	0.00
Teucrium chamaedrys	Lamiaceae	P	S	4.25	8.49	12.74	8.49	8.49	0.00	0.00	0.00
Thymus serpyllum	Lamiaceae	P	S	8.49	0.00	0.00	4.25	89.16	8.49	114.64	8.49
Tragopagon graminifolius	Asteraceae	P	F	4.25	0.00	8.49	4.25	21.23	4.25	25.48	0.00
Trifolium repens	Fabaceae	P	F	4.25	0.00	4.25	0.00	4.25	0.00	46.70	0.00
Trisetum rigidum	Poaceae	P	G	12.74	0.00	21.23	0.00	0.00	0.00	42.46	0.00
Urtica dioica	Urticaceae	P	F	16.98	0.00	4.25	0.00	4.25	0.00	12.74	0.00
Vicia persica	Papilionaceae	P	F	38.21	8.49	4.25	0.00	0.00	8.49	0.00	4.25
Viola odorata	Violaceae	P	F	8.49	0.00	0.00	4.25	114.64	0.00	123.13	0.00

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