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Prescribed burning and vegetation heterogeneity enhance predatory arthropod diversity in temperate dry grasslands

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Abstract

Background Temperate dry grasslands host diverse communities of predatory arthropods, yet their biodiversity is increasingly threatened by habitat degradation following the abandonment of traditional land-use practices. In many regions, restoring such practices is unfeasible or economically unsustainable, highlighting the need for an alternative, cost-effective, and ecologically sound management strategy. Prescribed burning has emerged as a promising tool to reduce accumulated biomass and limit shrub encroachment. However, scattered shrubs can also enhance habitat heterogeneity and buffer arthropods against climate extremes. Despite its growing use, the indirect effects of prescribed burning on invertebrate predators mediated through changes in vegetation structure remain poorly understood. In this study, we examined how prescribed burning, in combination with the presence of common hawthorn shrubs (*Crataegus monogyna* Jacq.), affects environmental conditions (i.e., litter cover and plant species richness) and the assemblages of spiders and ground beetles in temperate dry grasslands of the Dunajovice Hills National Nature Monument, Czech Republic. Predatory arthropods were sampled using pitfall traps across six sites, covering four treatments: burnt patches, burnt patches beneath hawthorn, control patches, and control patches beneath hawthorn.

Results We recorded 1703 spiders (107 species), 291 ground beetles (35 species), and 126 species of vascular plants. Burnt patches strongly favored xerothermophilous spider species, including several species of conservation concern. In contrast, burnt patches beneath hawthorns supported assemblages of moisture-habitat and shade-tolerant spider species, resulting in higher trait diversity (RaoQ). Control patches supported a greater proportion of shade-tolerant ground beetle species compared to burnt patches. Plant species richness was positively associated with spider species density, independent of treatment.

Conclusions Our findings demonstrate that prescribed burning can enhance predatory arthropod biodiversity in temperate dry grasslands, particularly when combined with the retention of scattered hawthorn shrubs. These results are directly applicable to land managers and conservation practitioners working in temperate, nutrient-poor dry grasslands, especially in regions where traditional land-use practices have declined. When applied in late winter, before peak arthropod activity, prescribed burning represents a cost-effective and ecologically viable management strategy for maintaining predatory arthropod diversity in both managed and abandoned dry grasslands.

Keywords Araneae, Carabidae, Common hawthorn, Conservation management, Czech Republic, Fire effects, Habitat heterogeneity, Trait-based diversity, Vascular plants

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Resumen

Antecedentes Los pastizales templados secos hospedan diversas comunidades de artrópodos predadores, aunque su diversidad está siendo incrementalmente amenazada por la degradación del hábitat que sigue al abandono de las prácticas tradicionales de uso de la tierra. En muchas regiones, la restauración de esas prácticas no es posible o es económicamente no sustentable, lo que subraya la necesidad de tener una estrategia alternativa, que sea costo-efectiva, y ecológicamente sensata. Las quemas prescriptas emergen entonces como una técnica promisoria para reducir la biomasa acumulada y limitar la invasión de arbustos. Sin embargo, arbustos aislados también pueden aumentar la heterogeneidad ambiental y proteger los artrópodos de extremos climáticos. A pesar de su uso creciente, los efectos indirectos de las quemas prescriptas sobre los predadores invertebrados mediados a través de cambios en la estructura de la vegetación, permanecen aún poco entendidos. En este estudio, examinamos cómo las quemas prescriptas, en combinación con la presencia de espino blanco o *crataegus* (*Crataegus monogyna* Jacq.), afecta las condiciones ambientales (i. e. la cobertura de mantillo y la riqueza de especies vegetales) y los ensambles de arañas y escarabajos del suelo en pastizales secos del Monumento Natural Nacional de las *montañas* de Dunajovice en la República Checa. Los artrópodos predadores fueron muestreados usando trampas pitfall a través de seis sitios, que cubrían cuatro tratamientos: parches quemados, parches quemados debajo de crataegus, parches control, y parches control debajo de crataegus.

Resultados Registramos 1.703 arañas (107 especies), 291 escarabajos de suelo (35 especies), y 126 especies de plantas vasculares. Los parches quemados favorecieron fuertemente las especies de arañas xero-termófilas, incluyendo varias especies que requieren de cuidados de conservación. En contraste, los parches quemados debajo de los crataegus contenían ensambles de arañas de lugares húmedos y tolerantes a la sombra, resultando en características de mayor diversidad (RaoQ). Los parches control contenían una mayor proporción de especies de escarabajos de suelo tolerantes a la sombra comparado con los parches quemados. La riqueza de especies vegetales fue asociada positivamente con la densidad de arañas, independientemente del tratamiento.

Conclusiones Nuestros resultados demuestran que las quemas prescriptas pueden incrementar la biodiversidad de artrópodos predadores en pastizales templados secos, particularmente cuando éstas se combinan con la retención de algunos ejemplares aislados de crataegus. Estos resultados son directamente aplicables para los gestores de tierras y quienes realizan prácticas de conservación, y que trabajan en pastizales templados, secos y pobres en nutrientes, en especial en regiones donde han declinado las prácticas de uso tradicional de la tierra. Cuando estas quemas se practican en el invierno tardío, antes del pico de la actividad de los artrópodos, pueden representar una estrategia costo-efectiva y ecológicamente viable para mantener la diversidad de artrópodos en pastizales secos templados, tanto en aquellos manejados como en los abandonados.

Background

Grasslands are among the most diverse ecosystems in Europe (Habel et al. 2013), with dry grasslands being particularly well known for their exceptionally high diversity of vascular plants (Janišová et al. 2011; Roleček et al. 2014). Temperate dry grasslands also play a crucial role in supporting arthropods, including many regionally rare and threatened species (Hamřík and Košulič 2021; Bauer et al. 2024). However, intensified agriculture has transformed grassland ecosystems into simplified croplands or abandoned, degraded areas (Matson et al. 1997; Tscharntke et al. 2005; Stoate et al. 2009), threatening arthropod biodiversity, including key natural enemies (Seibold et al. 2019; Raven and Wagner 2021; Prangel et al. 2023).

Most European dry grasslands are semi-natural and owe their existence to traditional land use, such as low-intensity grazing and/or mowing (Poschlod et al. 2002; Dengler et al. 2014; Roleček et al. 2014). Accordingly, grazing and mowing are now among the most common conservation management practices for Central European dry grasslands (e.g., Bonari et al. 2017; Řezáč and Heneberg 2019; Torma et al. 2023; Révész et al. 2024). In some regions, reintroducing traditional grassland farming practices is unfeasible or prohibitively expensive (Poschlod and Wallis De Vries 2002; Valkó et al. 2014), leading to a decline in the conservation value of formerly managed grasslands (Öckinger et al. 2006; Ruprecht et al. 2010; Hegedüšová et al. 2011). Consequently, conservationists face major challenges in identifying management tools that are both cost-effective and impactful for conserving grassland biodiversity. Prescribed burning could be a suitable and economical solution, with the potential to address key threats to European grasslands (Valkó and Deák 2021). In biodiversity conservation, prescribed burning refers to the controlled use of fire to enhance habitat conservation value by increasing environmental

heterogeneity and promoting plant and animal species richness through the reduction of dominant grasses and accumulated litter (Deák et al. 2014; Valkó and Deák 2021; Hamřík and Košulič 2021; Bonanomi et al. 2022).

Prescribed burning could also be an effective method for suppressing shrub encroachment in abandoned grasslands (Valkó et al. 2014). Common hawthorn (*Crataegus monogyna* Jacq.) is an early invader of abandoned grasslands (Fichtner and Wissemann 2021) and a potential target for removal by prescribed burning, yet it also supports biodiversity by providing nesting sites for birds, food resources for insects, plant protection from herbivores, and serving as a host plant for threatened moths (Kelemen et al. 2017; Fichtner and Wissemann 2021; Sitar et al. 2024). Such shrubs can also help arthropods cope with global warming by reducing ground temperatures and creating cooler, more humid microclimates during hot summers (Asmus et al. 2018; Gallé et al. 2024).

Spiders and ground beetles are dominant generalist predators (Lövei and Sunderland 1996; Nyffeler and Birkhofer 2017; Michalko et al. 2019) that respond predictably to small-scale changes in physical structure (Brose 2003; Kotze et al. 2011; Košulič et al. 2016; Hamřík and Košulič 2021) and microclimatic conditions, such as shading and humidity (Lövei and Sunderland 1996; Entling et al. 2007), as well as to the availability of their food resources (Uetz 1979; Carbonne et al. 2022; Michalko et al. 2021). Their species richness may be positively influenced by plant diversity (e.g., Taboada et al. 2010; Brunbjerg et al. 2018), reflecting a bottom-up effect (Farooq et al. 2022). In addition to supporting the availability of arthropod prey, more diverse plant communities exhibit greater structural complexity (Coverdale and Davies 2023), which supports predatory arthropods and provides refuge from intraguild predation (Langellotto and Denno 2004; Finke and Denno 2006; De Heij and Willenborg 2020). Although most ground beetles are generalist predators, they also include other trophic guilds, such as granivores and omnivores. These groups may respond positively to increased vegetation cover and benefit from the availability of weed seeds (De Heij and Willenborg 2020; Carbonne et al. 2022). The presence of litter is an important factor for many ground beetle and spider species, as it provides complex-structured microhabitats and favorable microclimatic conditions (Uetz 1979; Magura et al. 2003). Litter also serves as a habitat for one of the most important prey groups of these predatory arthropods – Collembola (Lawrence and Wise 2000; Bell 2001). Shrubs can enhance spider and ground beetle diversity by increasing habitat heterogeneity and offering refuge during hot summers (Schirmel et al. 2012; Spears and MacMahon 2012; Bennewicz and Barczak 2020; Gallé et al. 2024). Nevertheless, regionally threatened spiders and ground beetles are typically tied to disappearing xerothermic habitats with sparse vegetation and bare soil, and are negatively affected by humidity and shrub encroachment (Buchar and Růžička 2002; Řezáč et al. 2015; Buchholz et al. 2013; Schirmel et al. 2015; Bauer et al. 2024).

Spiders and ground beetles have been widely used in studies as suitable indicators for evaluating the effectiveness of grassland management approaches in conservation efforts. Previous research on the effects of grassland conservation management on spider and/or ground beetle biodiversity in Europe has predominantly focused on grazing and/or mowing (e.g., Lafage and Pétillon 2014; Bonari et al. 2017; Lyons et al. 2017; Torma et al. 2019; Torma et al. 2023; Révész et al. 2024). Despite the high potential of prescribed burning in dry grasslands for predatory arthropod conservation, only a few studies have investigated its effects in European dry grasslands (Valkó et al. 2016; Barber et al. 2017; Hamřík et al. 2021). To our knowledge, no research has examined predatory arthropod assemblages in patches beneath shrubs that have also been exposed to fire, leaving it unclear whether retaining scattered shrubs in burnt dry grasslands promotes biodiversity or whether their removal is more beneficial.

The objective of this study was to assess the effects of prescribed burning and habitat structure (i.e., litter cover, vegetation cover, and plant species richness) on spiders and ground beetles, with a particular focus on comparing burnt patches, patches beneath scattered *C. monogyna* within burnt sites, and their respective controls in southeastern Czech Republic. We hypothesized that (1) prescribed burning would reduce litter cover, leading to an increase in plant species richness. We also assumed that (2) increased plant species richness in burnt patches would enhance predatory arthropod diversity by increasing the availability of food sources, while exposed bare soil would promote xerothermophilous species of conservation concern. Finally, we predicted that (3) patches beneath *Crataegus monogyna* in burnt sites would support higher predatory arthropod diversity than adjacent open burnt patches and *C. monogyna* patches in unburnt control sites by offering more food resources and acting as refugia suitable for assemblages with different habitat affinities.

Methods

Study area

We carried out the study within Dunajovice Hills National Nature Monument (NNM) in the southeastern Czech Republic (Fig. 1). The Dunajovice Hills are located in one of the warmest areas of the Czech Republic with an average annual temperature exceeding 10 °C and the average annual precipitation is very low here, reaching values of less than 500 mm (Czech

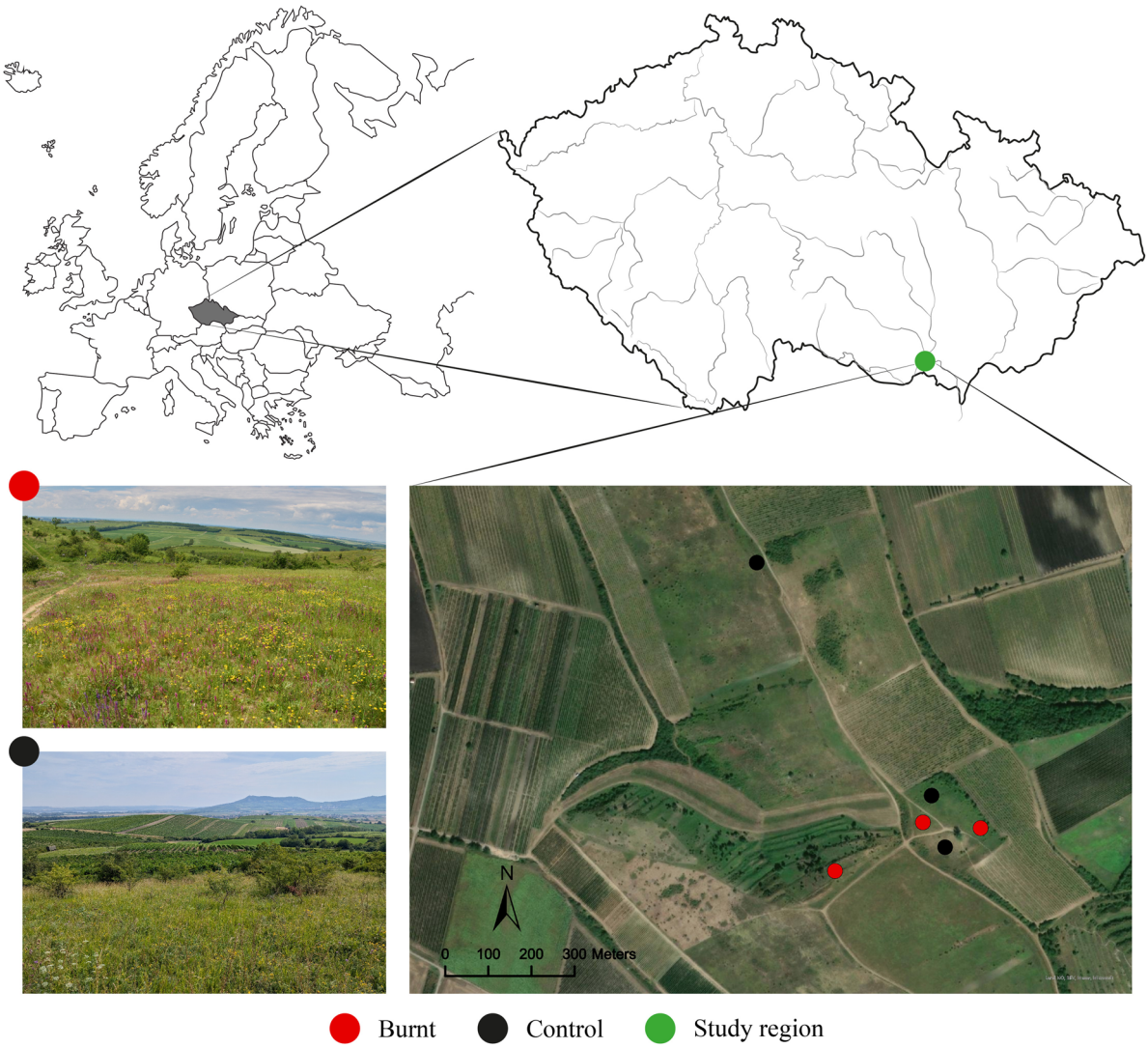

Fig. 1 Map of the study area with the positions of the 6 study sites

Hydrometeorological Institute 2025). The predominant bedrock in the hilly part of the area is Outer Flysch, consisting mainly of calcareous clays, claystones, sandstones, conglomerates, and menilite shales. The study area lies within the Chernozem soil region. The most widespread soil type on the Neogene sands is arenic chernozem, while typical chernozem occurs in areas with a preserved loess layer. On slopes and ridges, these are often replaced by eroded forms of these soils (Nature Conservation Agency of the Czech Republic 2019).

This is a biologically valuable area composed of a mosaic of broad-leaved and narrow-leaved dry grasslands, dry herbaceous fringes, and low xeric scrub as well as tall mesic scrub. The beginnings of nature conservation in the area of today's NNM date back to 1946; however, the area was granted the status of National Nature Monument in 1992. The area is also included in the Sites of Community Importance (Nature Conservation Agency of the Czech Republic 2019).

The dominant land use in the surrounding landscape is large-scale agriculture. The landscape of the Dunajovice Hills has also been shaped by centuries of traditional agricultural practices. Early agricultural settlers cleared the original forests and managed the land extensively, initially relying on grazing and mowing. Over time, they gradually transitioned to cultivating crops adapted to the local conditions. After World War II, a major turning point occurred with the displacement of the original population and the subsequent collectivisation of agriculture. Large areas of former agricultural land were abandoned. Nevertheless, some newly settled inhabitants soon

resumed viticulture on many previously cultivated plots, and to this day, parts of the Dunajovice Hills outside the NNM are still covered by vineyards. In contrast, the remaining parts of the area, most of today's NNM, were left fallow for years due to their unsuitability for intensive mechanized farming (Nature Conservation Agency of the Czech Republic 2019).

Study sites

The conservation management, mainly including mowing, grazing, and small-scale removal of woody vegetation, was implemented more extensively only after 1999. However, given the size of the protected area, the rapid rate of succession, and the already established populations of invasive plant species, the available financial resources were unfortunately far from sufficient to cover even the basic essential management of the most valuable parts of the NNM, particularly those hosting critically endangered species. As a result, most parts of the NNM have lacked adequate care for many years due to limited funding. It resulted in the implementation of the project titled "Restorative management of nationally important areas in South Moravia 2017–2022," funded by the Operational Programme Environment. The primary objective of the project was to halt the degradation of valuable plant communities in the Dunajovice Hills NNM through remedial interventions, including the removal of invasive tree species, the eradication of invasive plant populations, mowing, and grazing throughout the entire area. Therefore, we were unable to include control sites with no management over a 1-year period. However, the study sites were in comparable condition in terms of habitat structure prior to the experiment. After 1 year without conservation management, all sites had accumulated a substantial amount of dead plant biomass, which was subsequently reduced through prescribed burning (see Fig. 2). Winter or early spring prescribed burning is proposed as part of the conservation management plan to support biodiversity in the study area, as outlined in the Management Plan for the Dunajovice Hills NNM for the period 2020–2029 (Nature Conservation Agency of the Czech Republic 2019).

Study design

We selected six experimental sites consisting of dry grasslands within the protected area (48.8474325N, 16.5590650E; Fig. 1). The vegetation cover of the study sites was characterized by a mosaic of dry and semi-dry vegetation and low xeric scrubs, dominated by narrow-leaved grasslands (alliance *Festucion valesiacae*) and semi-dried broad-leaved grasslands (alliance *Cirsio-Brachypodion pinnati*). The altitude of the study sites varied from 273 to 282 m. Three sites were designated as burnt, with irregularly shaped burnt patches measuring 0.10 ha (site 1), 0.12 ha (site 2), and 0.15 ha (site 4), while the remaining three sites served as controls (site 3, site 5, site 6). The distance between burnt patches ranged from 50 to 200 m, while the distance between control patches ranged from 50 to 480 m. Prescribed burning (Fig. S1) was performed using drip torches and took place in February 2024, outside of the growing season.

- Broad-leaved dry grasslands – Site 1 (burnt), site 6 (control): Prior to our experiment, the sites were managed through extensive sheep and goat grazing, along with mosaic mowing and shrub reduction in 2022. However, these sites are located in the upper and marginal parts of the grazed locality, where livestock tend

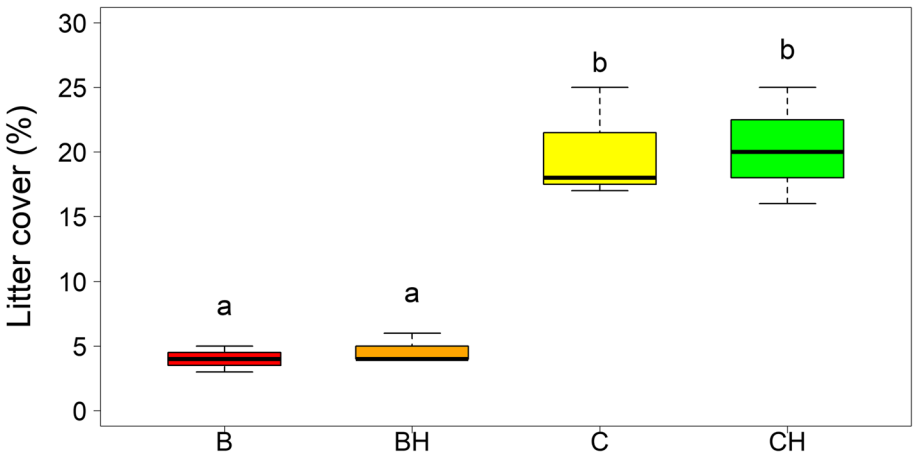

Fig. 2 The effect of treatment type on litter cover. B – burnt, BH – burnt hawthorn, C – control, CH – control hawthorn. The observation unit is a site. Horizontal lines within boxes indicate median values, box boundaries represent quartiles, and whiskers extend to 1.5 times the interquartile range. Statistically significant differences are indicated by different letters ($P < 0.050$)

to avoid grazing, concentrating instead in lower areas. Therefore, grazing intensity was likely low.

- Narrow-leaved dry grasslands – Site 2 (burnt): Prior to our experiment, the site was also subjected to prescribed burning at the end of winter in 2023, which was the first recorded management intervention. No formal conservation measures had been implemented previously; however, the site has a well-preserved character and contains only a small number of scattered shrubs. Site 3 (control): Prior to our experiment, this site was managed through mosaic mowing, with the most recent interventions conducted in 2022. Site 4 (burnt), and site 5 (control): Prior to our experiment, these sites were managed through mosaic mowing and shrub reduction, with the most recent interventions conducted in 2022.

Sampling protocol

We sampled spiders and ground beetles using pitfall traps made of 500-ml plastic cups (diameter: 9 cm, depth: 15 cm) without funnels or roofs, which were buried in the soil. We used 4% formaldehyde solution, supplemented with a few drops of an odorless detergent, as a killing and preserving agent.

We sampled spiders and ground beetles at six sites, comprising three sites with prescribed burning (burnt sites) and three unburnt control sites. At each burnt site, we established two treatment types: (1) burnt patches (grassland only) and (2) burnt patches beneath *C. monogyna* (hereafter referred to as burnt hawthorn). Similarly, at each control site, we established two corresponding treatments: (3) control (unburnt grassland) and (4) control patches beneath *C. monogyna* (hereafter referred to as control hawthorn). We selected one to five *C. monogyna* at each site, with individuals spaced at least 5 m apart, beneath which we placed pitfall traps (plots) positioned up to 60 cm from the trunk and oriented to the north. We placed pitfall traps at least 5 m from *C. monogyna* along transects in both burnt and control patches, with a minimum spacing of 5 m between traps within each treatment.

In the burnt sites (sites 1, 2, and 4), we used two traps per treatment at each site, resulting in six traps per treatment in total. In the control sites (sites 3, 5, and 6), the number of traps per treatment varied by site: site 3 had one trap per treatment, site 5 had five traps per treatment, and site 6 had two traps per treatment, yielding eight traps per treatment in total. The design was unbalanced due to the exclusion of one burnt site, which was initially sampled but later revealed to have mesic characteristics (e.g., nutrient-rich plant communities and overgrowth) that made it incomparable to the other nutrient-poor dry grasslands. As a result, we excluded two traps each from the burnt patches and burnt hawthorns. We placed the traps for two one-month periods, from May 15 to July 15, 2024. We preserved the collected specimens in 70% ethanol and stored them in the laboratory of the Faculty of Forestry and Wood Technology at Mendel University in Brno.

Environmental variables

We measured three environmental variables: (a) litter cover, (b) vegetation cover, and (c) plant species richness. We selected a hawthorn shrub with an associated pitfall trap and placed eight 2×2 m vegetation plots (relevés) around it. Four plots were located beneath the shrub canopy, and four were positioned in the open, 4 m from the shrub in each cardinal direction (north, south, east, and west). Within each plot, we identified all rooted vascular plant species, including herbs, grasses, and juvenile woody species, and visually estimated their cover. Plant species richness was recorded as the total number of vascular plant species per plot. Litter cover was estimated as the percentage of dead plant biomass (senescent grasses) from previous growing seasons in each plot. We then calculated the average values for each treatment within each site (Table S1).

Environmental data were collected in late July to early August 2024 to coincide with peak vegetation expression in dry grasslands. We found a positive correlation between vegetation cover and species richness of plants (Spearman correlation coefficient; rho = 0.63, $P = 0.029$). Thus, for further analysis, we used only the litter cover and species richness of plants.

Species classification

We identified all adult spiders to the species level following Heimer and Nentwig (1991) and Nentwig et al. (2024). The nomenclature is based on the latest version of the World Spider Catalog (2024). We identified ground beetle species following Müller and Motzfeld (2004); their nomenclature is based on Szél (2019). We identified plants following Kaplan et al. (2019).

We selected three species traits to characterize the trait diversity and trait composition of spiders and ground beetles: humidity preference (1 – very dry, 2 – dry, 3 – semi-humid, 4 – humid) and shading tolerance (1 – open, 2 – semi-open, 3 – partly shaded, 4 – shaded). For ground beetles, trophic guilds were considered as an additional trait (1 – phytophagous or granivorous, 2 – omnivorous, 3 – carnivorous). Spider species trait data were obtained from Buchar and Růžička (2002), while ground beetle species traits were sourced from various websites (Appendix 1). If a species was assigned to multiple categories, it received an average value. For non-integer

values between categories, we rounded based on expert knowledge. Traits of the recorded spider species are provided in Table S2, while traits of the recorded ground beetle species are presented in Table S3.

The classification of spider species as species of conservation concern was based on the Red List of Czech Spiders (Řezáč et al. 2015).

Statistical analyses

We quantified trait diversity using RaoQ, which measures trait dissimilarity between species weighted by their relative activity density (Botta-Dukát 2005; Mason et al. 2005; Villéger et al. 2008). We assessed trait composition using the community-weighted mean (CWM), which summarizes the average trait value weighted by the relative activity density of each species in the assemblage (Garnier et al. 2004). We calculated RaoQ using the "melodic" function (de Bello et al. 2016), and computed CWMs using the "functcomp" function from the "FD" package (Laliberté et al. 2025).

To test the effect of treatment type on predatory arthropods (activity density, species density, RaoQ, and CWM), we pooled the data across all sampling periods, resulting in one sample per trap and a total of 28 samples (i.e., 6 burnt patch, 6 burnt hawthorn, 8 control hawthorn, and 8 control patch). We performed the analyses using linear mixed-effects models (LMMs) implemented with the "lmer" function and generalized linear mixed-effects models (GLMMs) using the "glmer" function from the "lme4" package (Bates et al. 2025). Data with discontinuous distribution as counts (i.e., activity density and species density) were compared using GLMMs with a Poisson error structure (GLMM-p). If overdispersion was detected, GLMMs with a negative binomial error structure (GLMM-nb) were applied (Pekár and Brabec 2009). Normally distributed data (i.e., RaoQ, CWMs) were compared using LMMs. We evaluated the data at the trap level, with individual traps (data pooled across sampling periods) serving as replicates. Site ID (6 levels) was included as a random effect in all models.

We evaluated the effect of treatment type on litter cover, and the effects of both treatment type and litter cover on plant species richness. To assess how changes in environmental variables influence predatory arthropod diversity, we tested the interaction between treatment type and plant species richness on predatory arthropod species density. For this purpose, we evaluated the data at the site level by calculating the mean species density of each arthropod group (data pooled across sampling periods) and mean value of each environmental variable per treatment within each site (two treatments per site), resulting in 12 samples (i.e., 3 burnt patch, 3 burnt hawthorn, 3 control patch, and 3 control hawthorn). This averaging approach accounts for the unequal number of traps among treatments and ensures compatibility with the botanical data, which were collected using a different sampling design. Analyses were conducted using generalized linear models (GLMs). As the response variables were count data, models were initially fitted using a Poisson error structure (GLM-p). In cases where overdispersion was detected, negative binomial models (GLM-nb) implemented in the "MASS" package (Ripley et al. 2025) were employed (Pekár and Brabec 2009).

Post hoc comparisons were conducted using the "glht" function from the "multcomp" package (Hothorn et al. 2025).

We compared the composition of predatory arthropod assemblages between treatments using partial Redundancy Analysis (RDA) for spiders and Canonical Correspondence Analysis (CCA) for ground beetles. A pilot Detrended Correspondence Analysis (DCA) indicated the suitability of using Redundancy Analysis (RDA) for spiders and Canonical Correspondence Analysis (CCA) for ground beetles (Šmilauer and Lepš 2014). Only species occurring in more than three samples were included in the analysis. We applied Hellinger standardization of the data prior to Redundancy Analysis (RDA) and log $(y+1)$ transformation prior to Canonical Correspondence Analysis (CCA). Hellinger standardization is recommended for use with linear ordination methods (Legendre and Gallagher 2001). The significance of the effects was tested using Monte Carlo permutation tests with 999 permutations within the blocks represented by the sites.

We computed univariate analyses using R (R Development Core Team 2025) and performed multivariate analyses using CANOCO 5 (ter Braak and Šmilauer 2012).

Results

Environmental variables

We recorded a total of 126 vascular plant species. Treatment type affected the litter cover (GLM-p, $\chi^2_3 = 66.76$, $P < 0.001$), which was highest in control patches and beneath control hawthorns (Fig. 2). There was a significant negative relationship between plant species richness and litter cover (GLM-p, $\chi^2_1 = 6.04$, $P = 0.014$), with higher litter cover being associated with reduced plant species richness (Fig. 3). On the other hand, the treatment type did not affect the species richness of plants (GLM-p, $\chi^2_3 = 5.32$, $P = 0.150$; Table 1).

Spider diversity

We collected and identified 1703 specimens belonging to 107 species (Table S2). The most abundant species was

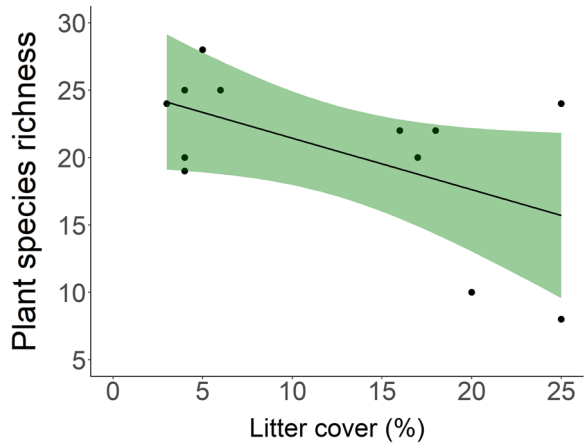

Fig. 3 The effect of litter cover on species richness of plants. The observation unit is a site. The colored bands represent the 95% confidence intervals

Pardosa lugubris (Walckenaer, 1802) ($n=370$; Lycosidae), *Zodarion rubidum* Simon, 1914 ($n=329$; Zodariidae), and *Aulonia albimana* (Walckenaer, 1805) ($n=198$; Lycosidae).

Treatment type had a marginal effect on activity density (GLMM-nb, $\chi^2_3=7.38$, $P=0.061$), with higher activity density in burnt hawthorns compared to burnt patches. The treatment type did not affect species density (GLMM-nb, $\chi^2_3=6.46$, $P=0.091$). The trait diversity (RaoQ) was different among treatments (LMM, $\chi^2_3=13.9$, $P=0.003$), with lower values observed in burnt patches compared to control patches and burnt hawthorns (Fig. 4a; Table 2).

The treatment type affected the CWM of humidity preference (LMM, $\chi^2_3=10.89$, $P=0.012$) and shading tolerance (LMM, $\chi^2_3=13.51$, $P=0.004$), with burnt hawthorns showing higher values than burnt patches (Fig. 4b and 4c; Table 2).

Spider species density was not significantly affected by the interaction between treatment type and plant species richness (GLM-p, $\chi^2_3=5.06$, $P=0.167$). However, plant species richness affected spider species density (GLM-nb, $\chi^2_1=4.88$, $P=0.027$), with an increase in plant species richness being associated with higher spider species density (Fig. 5).

Treatment type affected the spider assemblage composition (RDA, pseudo-F = 1.8, df = 3, $P=0.003$; Fig. 6), and explained 6.5% (adjusted R^2) of the compositional variability. The RDA biplot reveals that spider assemblages form four distinct groups, corresponding to each treatment. All treatments were associated with ground-dwelling species of conservation concern: Xerothermophilous species, such as *Civizelotes gracilis* (Canestrini, 1868), *Haplodrassus dalmatensis* (L. Koch, 1866) and *Phrurolithus pullatus* Kulczyński, 1897 were associated with burnt patches, while *Civizelotes pygmaeus* (Miller, 1943), *Haplodrassus kulczynskii* Lohmander, 1942, and *Thanatus arenarius* L. Koch, 1872 showed a preference for control patches. Xerothermophilous species, such as *Scotina palliardii* (L. Koch, 1881) and shade-tolerant *Talavera aperta* (Miller, 1971), were linked to burnt hawthorns, while shade-tolerant species such as *Bassaniodes robustus* (Hahn, 1832), *Agroeca cuprea* Menge, 1873, and moisture-habitat and shade-tolerant *Scotina celans* (Blackwall, 1841) were associated with control hawthorns.

Ground beetle diversity

We collected and identified 291 specimens belonging to 35 species (Table S3). The most abundant species were

Table 1 Effect of treatment type on environmental variables tested using GLMs. Significant results ($P < 0.050$) are shown in bold. Pairwise comparisons were conducted within "multcomp" package in R, using Tukey's adjustment for multiple comparisons. Values are presented on the model scale

Response variable	Treatment type	Estimate	Z	*P*
Litter cover	Burnt hawthorn–burnt	0.154	0.392	0.978
	Control–burnt	1.609	5.089	**< 0.001**
	Control hawthorn–burnt	1.626	5.149	**< 0.001**
	Control–burnt hawthorn	1.455	4.903	**< 0.001**
	Control hawthorn–burnt hawthorn	1.472	4.967	**< 0.001**
	Control hawthorn–control	0.017	0.091	1.000
Plant richness	Burnt hawthorn–burnt	−0.014	−0.084	1.000
	Control–burnt	−0.351	−1.899	0.228
	Control hawthorn–burnt	−0.237	−1.328	0.544
	Control–burnt hawthorn	−0.336	−1.817	0.264
	Control hawthorn–burnt hawthorn	−0.223	−1.245	0.598
	Control hawthorn–control	0.113	0.582	0.937

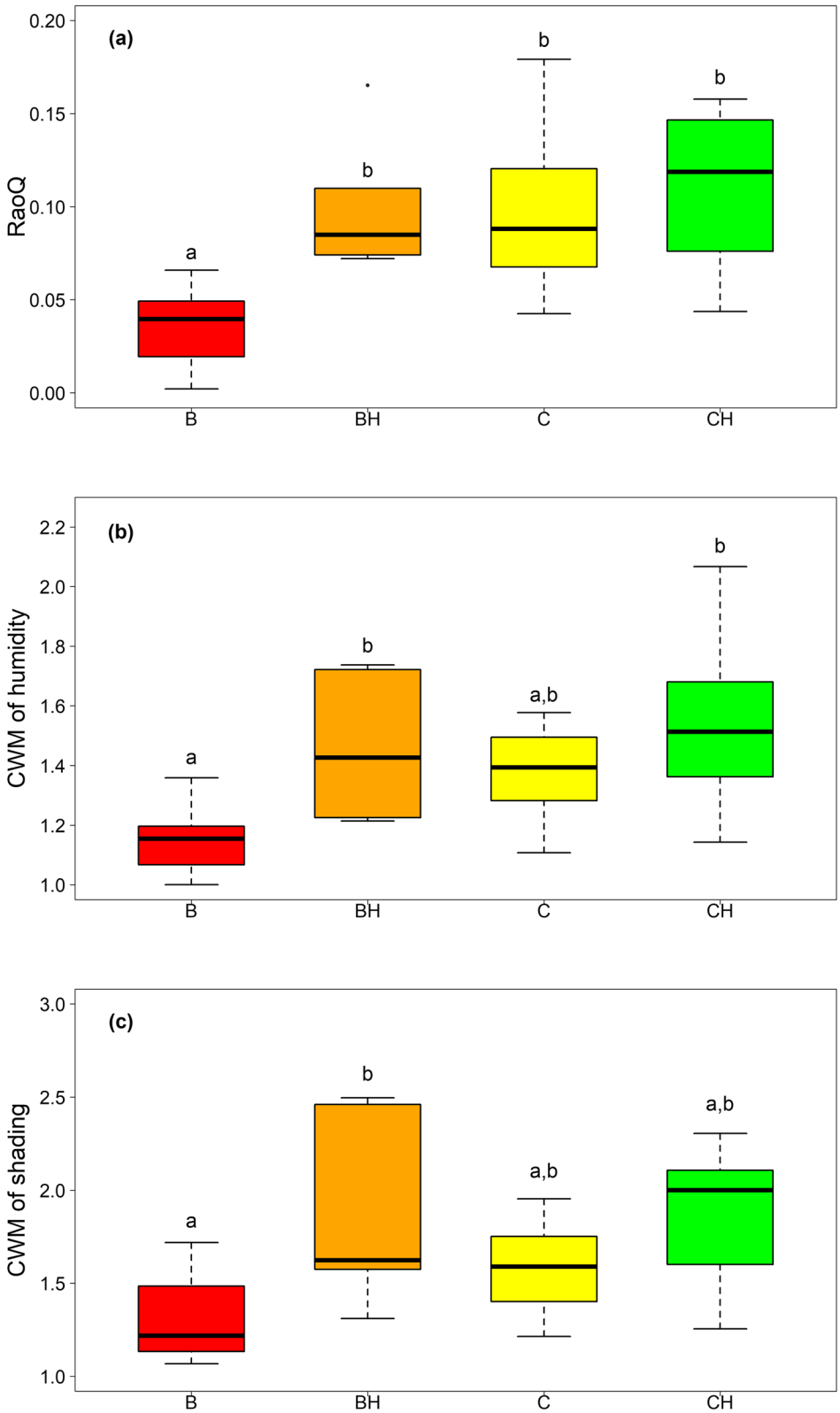

Fig. 4 The effect of treatment type on spider biodiversity: (**a**) trait diversity (RaoQ), (**b**) CWM of humidity preference, and (**c**) CWM of shading tolerance. B – burnt, BH – burnt hawthorn, C – control, CH – control hawthorn. The observation unit is a pitfall trap. Horizontal lines within boxes indicate median values, box boundaries represent quartiles, and whiskers extend to 1.5 times the interquartile range. Statistically significant differences are indicated by different letters ($P < 0.050$)

Table 2 Effect of treatment type on the biodiversity of spiders tested using LMMs and GLMMs. Significant results ($P < 0.050$) are shown in bold. Pairwise comparisons were conducetd within "multcomp" package in R, using Tukey's adjustment for multiple comparisons. Values are presented on the model scale

Response variable	Treatment type	Estimate	Z	P
Activity density	Burnt hawthorn–burnt	0.810	2.452	0.065
	Control–burnt	0.167	0.428	0.973
	Control hawthorn–burnt	0.561	1.477	0.443
	Control–burnt hawthorn	−0.643	−1.642	0.347
	Control hawthorn–burnt hawthorn	−0.249	−0.648	0.914
	Control hawthorn–control	0.394	1.468	0.448
Species density	Burnt hawthorn–burnt	0.281	1.691	0.308
	Control–burnt	0.002	0.009	1.000
	Control hawthorn–burnt	0.311	1.204	0.603
	Control–burnt hawthorn	−0.279	−1.081	0.682
	Control hawthorn–burnt hawthorn	0.030	0.119	0.999
	Control hawthorn–control	0.309	2.206	0.110
RaoQ	Burnt hawthorn–burnt	0.063	3.014	**0.014**
	Control–burnt	0.061	3.130	**0.009**
	Control hawthorn–burnt	0.075	3.842	**< 0.001**
	Control–burnt hawthorn	−0.002	−0.093	1.000
	Control hawthorn–burnt hawthorn	0.012	0.620	0.926
	Control hawthorn–control	0.014	0.769	0.868
CWM of humidity preference	Burnt hawthorn–burnt	0.303	2.783	**0.027**
	Control–burnt	0.211	1.894	0.229
	Control hawthorn–burnt	0.373	3.344	**0.005**
	Control–burnt hawthorn	−0.092	−0.822	0.843
	Control hawthorn–burnt hawthorn	0.070	0.627	0.923
	Control hawthorn–control	0.162	1.714	0.314
CWM of shading tolerance	Burnt hawthorn–burnt	0.541	3.618	**0.002**
	Control–burnt	0.227	1.010	0.729
	Control hawthorn–burnt	0.518	2.300	0.090
	Control–burnt hawthorn	−0.314	−1.394	0.483
	Control hawthorn–burnt hawthorn	−0.023	−0.104	1.000
	Control hawthorn–control	0.290	2.242	0.103

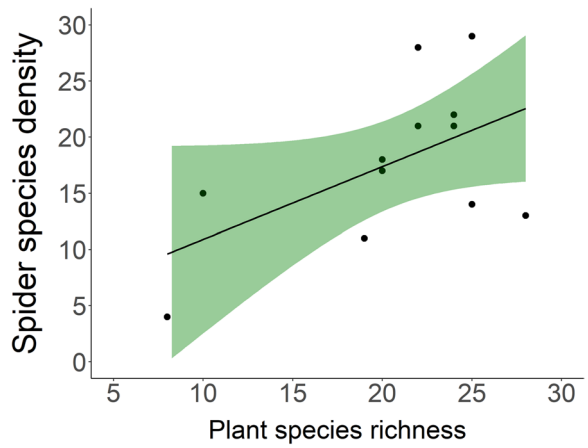

Fig. 5 The effect of plant species richness on spider species density. The observation unit is a site. The colored bands represent the 95% confidence intervals

Harpalus subcylindricus Dejean, 1829 ($n = 34$), *Harpalus rubripes* (Duftschmid, 1812) ($n = 33$), and *Harpalus caspius* Schauberger, 1928 ($n = 25$).

There was no effect of treatment type on activity density (GLMM-nb, $\chi^2_3 = 1.78$, $P = 0.618$), species density (GLMM-p, $\chi^2_3 = 2.95$, $P = 0.399$), trait diversity (LMM, $\chi^2_3 = 3.86$, $P = 0.277$; Table 3), and assemblage composition (CCA, pseudo-F = 1.1, df = 3, $P = 0.381$).

The treatment type did not have an effect on CWM of humidity preference (LMM, $\chi^2_3 = 2.72$, $P = 0.436$) and trophic guild (LMM, $\chi^2_3 = 5.02$, $P = 0.171$). However, the treatment type affected the CWM of shading tolerance (LMM, $\chi^2_3 = 8.79$, $P = 0.032$). Control patches had higher values than burnt patches (Fig. 7; Table 3).

There was no interaction between treatment type and plant species richness for ground beetle species density (GLM-nb, $\chi^2_3 = 4.02$, $P = 0.259$).

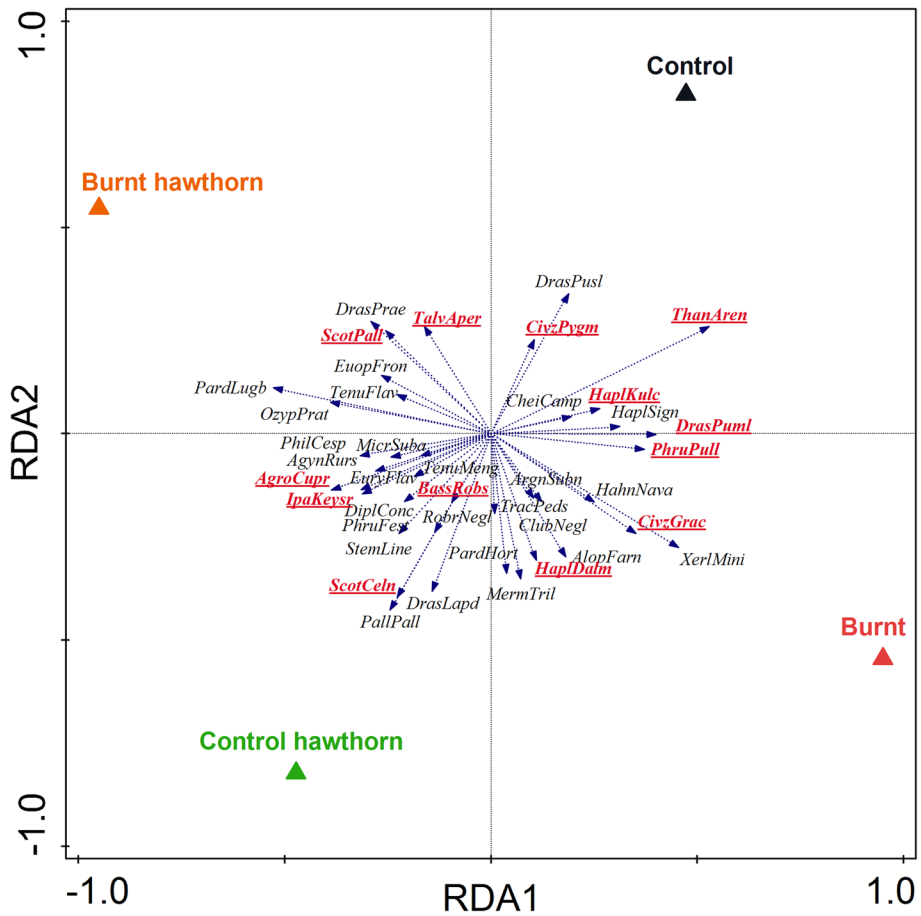

Fig. 6 Ordination diagram of Redundancy Analysis (RDA) showing the effect of treatment type on the assemblage composition of spiders. The first four letters of the genus and species are shown, with species of conservation concern highlighted in red and underlined

Discussion

We compared spider and ground beetle assemblages, along with environmental variables, across four treatment types: burnt patch, burnt hawthorn, control patch, and control hawthorn. We confirmed our first hypothesis that prescribed burning reduced litter cover; however, we did not find evidence that it led to increased plant species richness. Our second hypothesis was partially supported, as prescribed burning promoted the occurrence of species of conservation concern, particularly xerothermophilous spider species. Contrary to our expectations, spider trait diversity was lower in burnt patches compared to control patches. Although treatment type did not affect plant species richness, higher plant species richness was associated with increased spider species density. In support of our third hypothesis, burnt hawthorns hosted spider assemblages with higher shade and humidity tolerance, resulting in greater trait diversity than in adjacent burnt patches. However, the diversity of predatory arthropods in burnt hawthorns was comparable to that in control hawthorns.

Prescribed burning supports habitat specialist predatory arthropods

Prescribed burning did not significantly influence the species density of predatory arthropods; however, it reduced spider trait diversity in burnt patches. This outcome appears to be driven not by direct fire-induced mortality but by indirect ecological effects of the burn, namely, the simplification of habitat structure. These changes likely limited the availability of microhabitats required by trait-diverse spider assemblages and instead favored xerothermophilous ground-dwelling species, as reflected in the RDA biplot. This included several species of conservation concern (i.e., *C. gracilis*, *H. dalmatensis*, *P. pullatus*), consistent with previous findings on the positive effects of prescribed burning on rare and threatened xerothermophilous ground-dwelling spiders due to increased availability of bare substrate patches (e.g., Polchaninova 2013; Krause and Assmann 2016; Valkó et al. 2016; Hamřík and Košulič 2021). In contrast, control patches exhibited higher litter cover than burnt patches, which may have supported greater spider trait

Table 3 Effect of treatment type on the biodiversity of ground beetles tested using LMMs and GLMMs. Significant results ($P < 0.050$) are shown in bold. Pairwise comparisons were conducted within "multcomp" package in R, using Tukey's adjustment for multiple comparisons. Values are presented on the model scale

Response variable	Treatment type	Estimate	Z	P
Activity density	Burnt hawthorn–burnt	0.490	1.321	0.544
	Control–burnt	0.264	0.610	0.927
	Control hawthorn–burnt	0.173	0.392	0.979
	Control–burnt hawthorn	−0.226	−0.536	0.949
	Control hawthorn–burnt hawthorn	−0.317	−0.737	0.880
	Control hawthorn–control	−0.091	−0.273	0.993
Species density	Burnt hawthorn–burnt	0.418	1.685	0.330
	Control–burnt	0.267	1.104	0.686
	Control hawthorn–burnt	0.223	0.917	0.795
	Control–burnt hawthorn	−0.151	−0.707	0.894
	Control hawthorn–burnt hawthorn	−0.195	−0.901	0.803
	Control hawthorn–control	−0.043	−0.208	0.997
RaoQ	Burnt hawthorn–burnt	0.045	1.067	0.709
	Control–burnt	0.053	1.335	0.540
	Control hawthorn–burnt	0.082	2.074	0.161
	Control–burnt hawthorn	0.008	0.194	0.997
	Control hawthorn–burnt hawthorn	0.037	0.934	0.786
	Control hawthorn–control	0.029	0.798	0.855
CWM of humidity preference	Burnt hawthorn–burnt	0.184	1.277	0.557
	Control–burnt	0.143	0.650	0.909
	Control hawthorn–burnt	0.263	1.192	0.612
	Control–burnt hawthorn	−0.041	−0.185	0.998
	Control hawthorn–burnt hawthorn	0.079	0.357	0.983
	Control hawthorn–control	0.119	0.958	0.759
CWM of shading tolerance	Burnt hawthorn–burnt	0.207	0.961	0.771
	Control–burnt	0.630	3.122	**0.010**
	Control hawthorn–burnt	0.648	3.211	**0.007**
	Control–burnt hawthorn	0.423	2.095	0.154
	Control hawthorn–burnt hawthorn	0.441	2.184	0.127
	Control hawthorn–control	0.018	0.096	1.000
CWM of trophic guild	Burnt hawthorn–burnt	0.122	0.598	0.928
	Control–burnt	−0.022	−0.072	1.000
	Control hawthorn–burnt	0.374	1.230	0.590
	Control–burnt hawthorn	−0.144	−0.473	0.962
	Control hawthorn–burnt hawthorn	0.252	0.828	0.831
	Control hawthorn–control	0.396	2.239	0.104

diversity by providing a more complex habitat and more stable microclimatic conditions (Bell 2001). Moreover, increased litter levels enhance soil moisture retention in dry grasslands (e.g., Deutsch et al. 2010), which may, in turn, enrich local xerothermophilous species assemblages by facilitating the occurrence of moisture-habitat species. However, the CWM of humidity preference did not differ significantly among these treatments.

Ground beetles in burnt patches exhibited lower shading tolerance than those in control patches. Prescribed burning primarily supports open-habitat ground beetle species (e.g., Martikainen et al. 2006; Bargmann et al. 2015), whereas habitat generalists prefer shrub-encroached dry grasslands with high litter accumulation (Schirmel et al. 2015). This pattern may, therefore, be explained by the lower amount of litter and standing

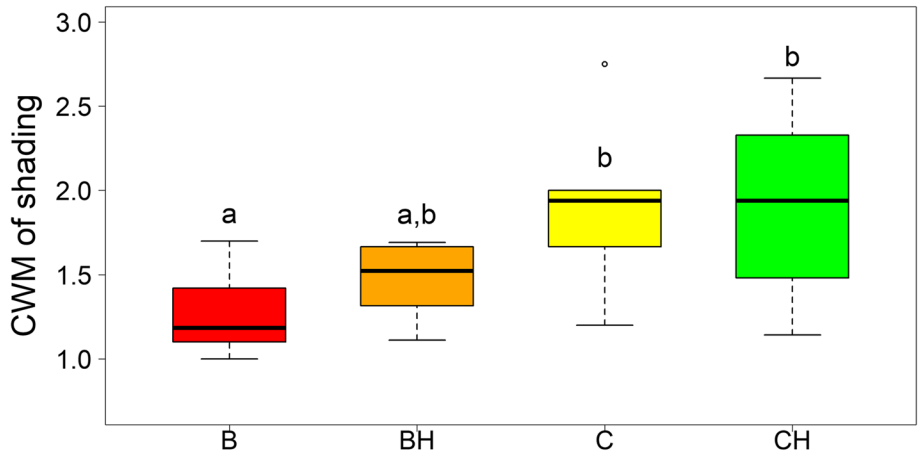

Fig. 7 The effect of treatment type on CWM of shading tolerance of ground beetles. B – burnt, BH – burnt hawthorn, C – control, CH – control hawthorn. The observation unit is a pitfall trap. Horizontal lines within boxes indicate median values, box boundaries represent quartiles, and whiskers extend to 1.5 times the interquartile range. Statistically significant differences are indicated by different letters ($P < 0.050$)

dead plants in burnt patches, which likely does not support the occurrence of shade-tolerant habitat generalists. On the other hand, shade-tolerant species found beneath burnt hawthorns likely benefited from the shaded environment provided by the shrubs, which may also explain their similar CWM of shading tolerance to that of control hawthorns.

The presence of scattered hawthorns enhances spider diversity

Burnt hawthorns supported marginally higher spider activity density and a greater proportion of shade-tolerant and moisture-habitat spider species compared to burnt patches. This likely contributed to the greater trait diversity of spiders observed in this treatment. The sparse vegetation and harsh microclimatic conditions in the burnt patches may act as an environmental filter, resulting in the predominance of a specialist species, which could explain the lower trait diversity observed. In contrast, scattered shrubs enhance both thermal and moisture heterogeneity, buffering extreme microclimatic fluctuations and thus facilitating the persistence of diverse arthropod communities (Gallé et al. 2024). Moreover, the greater structural complexity beneath hawthorns likely provides an increased number of available niches. Habitat complexity created by scattered shrubs is also known to promote diverse spider assemblages (Gallé et al. 2017) and to increase prey availability (Spears and MacMahon 2012; Diehl et al. 2013). Another possible explanation is that hawthorn shrubs may have served as refuges for shade-tolerant spider species that lost their shaded environment in the burnt patches, potentially triggering a spillover into the nearby hawthorns. A decline in habitat quality in managed areas can lead to spillover into more suitable habitats (Tölgyesi et al. 2018; Hamřík et al. 2023).

Burnt and control hawthorns exhibited comparable diversity of predatory arthropods and provided suitable microhabitats for several spider species of conservation concern with affinities for moisture and shade (i.e., *S. celans*, *T. aperta*, *B. robustus*). These species are typically found beneath stones or within litter (Buchar and Růžička 2002). This suggests that scattered hawthorns play an important role in supporting predatory arthropod diversity in dry grasslands.

Species richness of plants increases spider diversity

Although our study did not detect a treatment-specific increase in plant species richness, our results demonstrated a positive relationship between plant species richness and spider species density, whereas no such pattern was found for ground beetles. This pattern aligns with findings that highlight stronger links between plant diversity and spiders than with ground beetles (Brunbjerg et al. 2018; Li et al. 2018), likely due to a bottom-up effect (Farooq et al. 2022).

These bottom-up effects may result from increased food web complexity and microhabitat heterogeneity. Greater plant diversity is often positively associated with increased structural complexity (Coverdale and Davies 2023), which offers more niches and microhabitats for both spiders and their prey (Langellotto and Denno 2004). For instance, plant species richness is positively associated with Collembola diversity (Sabais et al. 2011), a key prey group for spiders (Lawrence and Wise 2000; Bell 2001). This is presumably due to the greater range of food resources provided by diverse plant communities (Sabais et al. 2011).

Plant species richness was positively correlated with overall vegetation cover. Previous studies have shown that increased vegetation cover can benefit granivorous and omnivorous ground beetles by enhancing the availability of food resources, such as seeds (De Heij and Willenborg 2020; Carbonne et al. 2022). In our study, prescribed burning did not significantly alter plant species richness, which likely explains the absence of clear treatment effects on the distribution of ground beetle trophic guilds. From a fire ecology perspective, this suggests that the low-intensity, winter burns used here did not substantially alter ground-layer resource dynamics, highlighting how fire regime characteristics can mediate bottom-up effects on arthropod communities.

Litter cover can negatively affect plant species richness by reducing seed germination (e.g., Xiong and Nilsson 1999); therefore, litter-reducing disturbances such as prescribed burning can promote plant diversity, which may subsequently enhance predatory arthropod diversity. Although we found a negative relationship between litter cover and plant species richness, we cannot determine whether this pattern was directly caused by the suppressive effect of litter on germination.

Limitations of the study and directions for future research

We acknowledge the concern regarding the 5-m spacing between pitfall traps within treatments, as a greater distance is generally recommended to ensure traps are treated as independent samples (e.g., Digweed et al. 1995). However, we analyzed the data at the trap level to retain the fine-scale spatial resolution necessary for detecting localized treatment effects, particularly given the patchy nature of post-burn microhabitats and the contrasts between open and shrub-covered patches. This trap-level sampling design is consistent with common practice in arthropod ecology, especially in studies targeting fine-scale habitat variation (e.g., Schirmel et al. 2015; Hamřík and Košulič 2021; Torma et al. 2023; Gallé et al. 2024).

We recognize that the selection of species traits can influence the outcomes of trait-based community analyses. However, trait availability remains limited for spiders and ground beetles (e.g., humidity preference, shading tolerance, trophic guild, vertical stratum preference, hunting strategy, body size, and dispersal ability). Due to the nature of pitfall trapping, traits like stratum preference and hunting strategy were less informative, as our method predominantly sampled ground-dwelling active hunters while underrepresenting herb-dwelling and web-building spiders. Body size, though frequently applied in trait-based studies, is shaped by multiple factors (e.g., prey availability, microclimate), which can complicate the interpretation of results (Gallé and Batáry 2019). Dispersal ability is more relevant in studies spanning larger spatial scales (e.g., Gallé et al. 2018; Hamřík et al. 2023); however, our treated sites were close to unmanaged sites, which likely minimized any effect of species-specific dispersal limitations. Accordingly, this trait would be particularly relevant for studies on prescribed burning conducted at larger spatial scales or in a landscape-context framework.

To gain a more comprehensive understanding of the ecological effects of prescribed burning on arthropod communities, future studies should incorporate larger-scale treatments. Furthermore, there is currently a lack of knowledge regarding the size of burnt patches and how this interacts with vegetation type. Such investigations are essential for developing effective fire management strategies that promote biodiversity while minimizing unintended ecological consequences.

Implications for fire and environmental management

Our findings have several important implications for fire-informed conservation and policy in temperate dry grasslands. First, prescribed burning, when carefully timed and applied at appropriate intensities, can be a valuable management tool for promoting xerothermophilous arthropod species of conservation concern. Second, the retention of scattered shrubs such as *Crataegus monogyna* enhances microclimatic and structural habitat diversity, supporting both shade-tolerant and moisture-habitat species. These shrubs can act as fire-resilient microhabitat refugia, offering essential conditions for species persistence during and after fire events (e.g., Asmus et al. 2018; Gallé et al. 2024). Rather than being uniformly removed, such structures should be recognized as integral components of post-burn habitat mosaics, contributing to the biodiversity value of a site (e.g., Oksuz et al. 2020). From a policy perspective, integrating prescribed fire into conservation strategies requires site-specific fire regime guidelines that reflect ecological goals (e.g., Valkó et al., 2021). Management plans should adopt adaptive fire regimes modulating fire frequency, intensity, and seasonal timing while preserving structural refuges like shrubs or unburnt patches. This dual approach supports both specialist and generalist species, increases ecosystem heterogeneity, and helps mitigate the risk of uncontrolled wildfires in abandoned or fuel-loaded grasslands (Valkó and Deák 2021; Salis et al. 2022). As traditional grazing and mowing become less feasible in many European regions, prescribed fire offers a cost-effective,

ecologically justified tool to sustain biodiversity and ecosystem functions, with strong potential for wider application across dry grassland systems.

Conclusions

Our study demonstrates that prescribed burning and the presence of scattered hawthorn shrubs influence predatory arthropod assemblages in dry grasslands in distinct but complementary ways. Burnt patches exhibited lower trait diversity of spiders compared to control patches, likely due to the creation of conditions favoring primarily xerothermophilous spider species. These outcomes likely reflect short-term post-fire dynamics, whereas longer-term processes may promote the recovery of spider trait diversity through spider recolonisation and vegetation regrowth. While direct mortality from the fire was not assessed, the observed patterns suggest that trait filtering via changes in vegetation and microclimate exerts a stronger influence than any immediate fire-induced mortality. In contrast, scattered hawthorns supported moisture-habitat and shade-tolerant species and increased spider trait diversity within burnt sites. Notably, both prescribed burning and scattered hawthorns supported spider species of conservation concern. Although the treatment did not affect plant species richness, higher plant species richness was positively associated with spider species density. This pattern suggests that vegetation diversity plays an essential role in supporting higher trophic levels through bottom-up processes, likely by increasing structural complexity, prey availability, and niche diversity for predatory arthropods.

The responses of ground beetles were less clear, likely due to their broad and variable habitat requirements (Kotze et al. 2011; Čížek et al. 2012), which may have facilitated movement among treatments. Additionally, their lower activity levels compared to spiders may have reduced detectability and contributed to the observed patterns.

Our findings suggest that prescribed burning can be an effective conservation management strategy in dry grasslands, particularly for supporting grassland habitat specialists. Furthermore, the presence of scattered shrubs, such as hawthorns, plays a crucial role in enhancing spider diversity by improving habitat complexity and microclimatic conditions. To optimize these outcomes, future management should consider the intensity of prescribed burning and the density or spatial arrangement of shrubs, as overly intense burns or excessive shrub cover may reduce habitat suitability for certain species or undermine the benefits of microhabitat heterogeneity.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-025-00409-9.

Additional file 1: Appendix 1: Websites providing ground beetle species trait data.

Additional file 2: Table S1 Values of environmental variables in study sites.

Additional file 3: Table S2 List of recorded spiders with species traits. Humidity preference: very dry (1), dry (2), semi-humid (3), humid (4); shading tolerance: open (1), semi-open (2), partly-shaded (3), shaded (4)

Additional file 4: Table S3 List of recorded ground beetles with species traits. Humidity preference: very dry (1), dry (2), semi-humid (3), humid (4); shading tolerance: open (1), semi-open (2), partly-shaded (3), shaded (4); and trophic guild: phytophagous or granivorous (1), omnivorous (2), carnivorous (3)

Additional file 5: Fig. S1 Images illustrating fire intensity and the burning of scattered hawthorns

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT to correct English. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Clinical trial number

Not applicable.

Authors' contributions

T.H., O.K., and R.G. contributed to the conception and design of the study. T.H. and O.K. collected predatory arthropods and conducted spider identification, while M.Z.S. was responsible for ground beetle identification. J.Š. collected environmental data and conducted plant identification. T.H. analyzed the data and wrote the main manuscript text. O.K., R.G., J.Š., and M.Z.S. provided comments on the manuscript. All authors read and approved the final version of the manuscript.

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Data availability

The data that support the findings of this study are available in the supplementary material of this article.

Declarations

Ethics approval and consent participate

Not applicable.

Consent for publication

Not applicable.

Competing Interests
The authors declare no competing interests.

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