

Summer fire in steppe habitats: long-term effects on vegetation and autumnal assemblages of cursorial arthropods

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Abstract

Being an essential driving factor in dry grassland ecosystems, uncontrolled fires can cause damage to isolated natural areas. We investigated a case of a small-scale mid-summer fire in an abandoned steppe pasture in northeastern Ukraine and focused on the post-fire recovery of arthropod assemblages (mainly spiders and beetles) and vegetation pattern. The living cover of vascular plants recovered in a year, while the cover of mosses and litter remained sparse for four years. The burnt site was colonised by mobile arthropods occurring in surrounding grasslands. The fire had no significant impact on arthropod diversity or abundance, but changed their assemblage structure, namely dominant complexes and trophic guild ratio. The proportion of phytophages reduced, while that of omnivores increased. The fire destroyed the variety of the arthropod assemblages created by the patchiness of vegetation cover. In the post-fire stage they were more similar to each other than at the burnt plot in the pre- and post-fire period. Spider assemblages tended to recover their pre-fire state, while beetle assemblages retained significant differences during the entire study period.

Izvleček

Nenadzorovani požari na suhih traviščih so ključni dejavnik, ki lahko povzroča škodo v izoliranih naravnih območjih. Preučevali smo primer malopovršinskih požarov, ki nastanejo sredi poletja na opuščeni stepskih pašnikih v severovzhodni Ukrajini. Osredotočili smo se na obnovo združb členonožcev (predvsem pajkov in hroščev) in vegetacije po požaru. Pokrovnost vegetacije se je obnovila po enem letu, pokrovnost mahov in opada pa je ostala redka po štirih letih. Pogorelo rastišče so naselili mobilni členonožci iz sosednjih travnikov. Požar ni imel pomembnega vpliva na raznolikost in pogostnost členonožcev, a je spremenil strukturo njihovih združb, predvsem dominanco in deleže prehranjevalne združbe. Delež fitofagov se je zmanjšal, omnivorov pa se je povečal. Požar je uničil številne združbe členonožcev, ki so nastale v različnih zaplatah vegetacije. V fazah obnove po požaru so si bile bolj podobne kot ploskve pred in po požaru. Združbe pajkov so se obnovile v stanje pred požarom, medtem ko so združbe hroščev ostale značilno različne celotno obdobje raziskave.

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Introduction

Fire and grazing are the major disturbance factors shaping grassland ecosystems. They can prevent woody plant encroachment, inhibit expansion of invasive species and, if applied extensively, promote the growth of herbaceous vegetation (Collins 2000, Peterson & Reich 2008, Ladwig et al. 2018). Their complex interaction results in vegetation heterogeneity (Fuhlendorf & Engle 2004, Doxon et al. 2011) and shifting mosaics of habitats and food resources for primary consumers (Whiles & Charlton 2006). Nevertheless, an increase of frequency and intensity of fire as a result of reduced grazing can have a negative impact on various components of grassland biota and the ecosystem as a whole (Pereira et al. 2017). This process is driven by both global climate change (Dube 2009, Koltz et al. 2018) and local changes in grassland management (Samu et al. 2010, Polchaninova et al. 2016a, Savchenko & Ronkin 2018, Torma et al. 2019). Traditional pastoralism had been a common practice in European grasslands until the end of the 20th century. Now many countries are facing pasture abandonment and an increase of uncontrolled grassland fires (Polchaninova 2015, Valkó et al. 2016, Kertész et al. 2017).

The effect of fire is well studied in prairie ecosystems, including its impact on arthropod communities (Allen & Palmer 2011, Kral et al. 2017). Prescribed burning has long been used as a management tool in tallgrass prairies (see Limb et al. 2016), which encouraged comprehensive studies of its impact on rangeland ecosystems (Fuhlendorf & Engle 2004, Debinski et al. 2011, Milberg et al. 2014, Kral et al. 2017). In Europe this practice is rarely applied (Valkó et al. 2014); thus, consequences of burning are poorly known. Moreover, the large variety of climatic conditions and grassland types, from alkaline grasslands in Hungary (Valkó et al. 2016) to mesic meadows in southern Sweden (Milberg et al. 2014), makes it difficult to apply experience gained in one system to another.

There is no practice of prescribed burning in Ukraine, despite the fact that in recent decades the fires have become more frequent and encompassed larger areas. Moreover, burning in protected areas is prohibited by law. Before recommending (or advising against) fire as grassland management or conservation tool, thorough research of its consequences on local and landscape scale is strictly required. Wildfires provide natural experiments for investigations, being variable in season, frequency, intensity and extent.

The effect of fire on grassland vegetation is better studied and understood (Vermeire et al. 2011, Chibilev 2014, Kertész et al. 2017) than its influence on invertebrate communities (Kral et al. 2017, Koltz et al. 2018). The

response of the latter is highly variable and can be negative, neutral or positive within the same systematic or ecological group living in similar environmental conditions (Swengel 2001, Panzer 2002, Wade & Roughley 2010, New 2015). Therefore, there is no simple answer to the question of how fire affects invertebrates (New 2015, Kral et al. 2017), since it depends on covariant external drivers (history of fire events, season, intensity and extent, land use, landscape habitat mosaic, weather conditions etc.) as well as species characteristics (dispersal mobility, life stage, habitat and feeding preferences).

The post-fire recovery of arthropod assemblages is often driven by the recovery of vegetation structure and species composition as it alters microenvironment, provides shelters and food resources and influences competitive relations (Engle et al. 2008, Engstorm 2010, Koltz et al. 2018). Thus, the multi-taxon study of arthropod communities in connection with vegetation changes is the most promising direction in the research of post-fire recovery of grassland ecosystems.

In the East European Plain, research on the fire ecology of dry grassland arthropods is at an initial stage (see Polchaninova et al. 2016b). We investigated a case of small-scale summer fire at a long-term monitoring site in the gully steppe in northeastern Ukraine. This paper presents the first results of a comprehensive study of the post-fire plant and arthropod recovery. Here we focused on two questions: (1) What arthropods are the first to colonise the burnt steppe? and (2) How do their assemblages change in the post-fire period? Since the fire occurred in summer, we regarded only autumnal assemblages and investigated the following taxonomic groups: Araneae, Coleoptera, Homoptera and Orthoptera. In the end of the growing season, we did not expect newborn imagoes of insects whose larvae develop in the soil; therefore, all the arthropods had to have survived the fire in soil cracks or other shelters or colonised the burnt plot.

Material and methods

Study area and fire events

The research was carried out in the Regional Landscape Park ‘Velykoburlutskyi Steppe’ (Kharkiv Region, north-eastern Ukraine). Its land use history, relief, flora and vegetation were described in detail in a previous publication (Ronkin & Savchenko 2016). The park includes a net of gullies covered with virgin steppe vegetation on the upper parts of the slopes and with dry or mesic meadow vegetation on the lower parts of the slopes and in the bottoms. Such a landscape unit is called “gully steppe”. The site has been constantly monitored since 1991. Moreover,

we interviewed the villagers about the former economical use of the study area (from 1940 to 1990). The material discussed in the present paper was collected on the top of a steppe slope (49.93040 N; 37.30956 E). This slope was under moderate cattle grazing until 2005, when the grazing intensity dropped dramatically. As of 2013, the pasture has been completely abandoned. Currently the vegetation is mainly represented by forb-fescue and/or forb-fescue-feather grass communities (*Festucion valesiacae* Klika 1931, *Festuco-Brometeta*).

One of the phenological peculiarities of the abandoned steppe plots of the study area is an early end of the growing season in mid-July to early August (Savchenko & Ronkin 2018). At that time the fire risk period begins and lasts until late November. Another period of fire hazards is spring (after the snow melt in late February to April). Nowadays almost all fires in the area are ignited by human activity, either accidentally or intentionally. In both cases they are not under control.

The fire in question occurred on 20 July 2014 and encompassed about three hectares of the steppe slope (Figure 1). According to our 25-year monitoring, it was the first fire event at this plot.

Sampling design

The investigation of the study plot can be divided into two periods: In 2013 the research aim was to identify the arthropod diversity and abundance as part of the general inventory of the steppe biota of the landscape park. After

the spontaneous fire we continued our investigations aiming at the comparison of the vegetation and arthropod assemblages in the pre- and post-fire years. Besides the study plot (SP) (aspect 120°, inclination 12°), we included into the study a plot not affected by the fire, hereinafter referred to as “conditional control” (CC). It is located on the top of the same slope at a distance of 3 m from the edge of the study plot (aspect 105°, inclination 8°). Being different in dominant species and vegetation structure, CC was the only unburnt plot in the close proximity that was similar to SP in the species composition of vascular plants. This plot was investigated not only for the comparison, but also for the vegetation and arthropod monitoring to avoid misinterpreting natural annual fluctuations as consequences of the fire event.

Arthropods collection

We collected cursorial arthropods by pitfall trapping using 6.5 cm diameter plastic cups half-filled with 4% formalin. In 2013 we placed a line transect of 10 traps with 10 m spacing between the traps along the top slope. The traps were emptied once a month from late April to early October, with a break from early August to early September. The material obtained monthly from one trap was considered as a subsample, and the ten subsamples were combined as a sample.

In the post-fire period (from September 2014 to October 2018) we used the same transect as in 2013 and placed five triplets of pitfall traps at a distance of 10 m



Figure 1: Burnt slope three days after the fire, July 2014. Regional Landscape Park ‘Velykoburlutskiy Steppe’. Photo: Vladimir Ronkin.
Slika 1: Požgano pobočje tri dni po požaru, julij 2014. Regionalni krajinski park ‘Velykoburlutskiy Steppe’. Foto: Vladimir Ronkin.

from each other. A triplet (three traps established three metres apart perpendicular to the transect) was considered as a subsample, while five triplets made one sample. The plot of conditional control (CC) was so small that there was space for only three triplets. The distance between the nearest triplets of pitfall traps at the burnt and unburnt plots (SP vs CC) was about 35 m. Thus, the samples by plots/years were as follows: SP13 – study plot before the fire in 2013 (unburnt); SP14, SP15, SP16 and SP18 – study plot after the fire event in 2014, 2015, 2016 and 2018 (burnt); CC14, CC15, CC16 and CC18 – plot of conditional control in the corresponding years (unburnt). The design was adopted from Samu et al. (2010); it provides replicates for the statistical analysis and, compared with one trap, diminishes the risk of accidental individual presence/absence in subsamples.

Before the fire autumnal collecting was conducted during 07.09–09.10.2013 and after the fire during 06.09.–12.10.2014, 13.09.–10.10.2015, 10.09.–4.10.2016 and 10.09.–08.10.2018. The total material included 386 spiders, 999 beetles, 389 acridids, 222 leafhoppers and 87 individuals of other insects.

Vegetation samples

Vegetation characteristics were estimated in late July to early August on 3.16 m × 3.16 m quadrats. Such a quadrat was proven to be an important grain size in a nested set of seven plot sizes (0.0001–100 m²) used in the standardised EDGG sampling methodology (Dengler et al. 2016). Moreover, it was the most convenient quadrat size given the distance between pitfall traps for the arthropod collection in our design.

We obtained the following data: (1) total cover, (2) living cover of vascular plants, (3) cover of litter, (4) cover of mosses, (5) cover of three herb layers (the highest, the shortest and the intermediate one), (6) height of the layers and (7) main species of the herb layers (those having ³5% cover). In total, 48 estimations of these characteristics were made. We sampled six quadrats at SP before the fire, six at CC in 2014 shortly after the fire and six quadrats at each plot (SP and CC) in 2015, 2016 and 2018. The height of the herb layers was measured at five randomly selected points in each quadrat. The quadrats were placed at a distance of 10 m from each other, nine of them in close proximity to each subsample of pitfall traps for the arthropods collection and three between the nearest triplets of pitfall traps at SP and CC. We indicated the main plant communities in the sampled area (SP + CC) by listing their dominants in decreasing order.

We registered all vascular plant species growing at SP and CC in order to evaluate the plots' floristic similarity.

Additionally, we compared the floristic composition of SP and the other two unburnt plots, located in the bottom and on the south-facing slope of the same gully at a distance of more than 100 m from SP.

Data analysis

Adult spiders were identified to the species level, juveniles to the family level. Imagoes of the true bugs (Heteroptera) and beetle families Carabidae, Dermestidae, Tenebrionidae, Silphidae and Coccinellidae were also identified to the species, while other beetles to species, genus or only family level. The Homoptera (juvenile Cicadinea) and Orthoptera (Acridoidea) were counted and regarded as groups at the order level. Although pitfall trapping is not the best method for leafhopper and grasshopper censuses, they often comprise a significant part of invertebrates collected with traps, giving sufficient comparative material. We compared assemblage structures of spiders and beetles and included other insects in the analysis of trophic preferences.

Arthropod abundance was estimated as activity density (number of individuals/100 trap-days). Since both the individual abundance of arthropods and the vegetation parameters differed significantly from normal distribution ($P < 0.05$, Shapiro-Wilk and Kolmogorov-Smirnov normality tests), the U-test (Mann-Whitney) and Kruskal-Wallis ANOVA on ranks were applied when comparing vegetation and arthropod assemblages per plot or year. Statistical significance was set at $P < 0.05$.

Correspondence Analysis ordination of the study and conditional control plots regarding the time since fire was based on vegetation parameters (total vegetation cover, living cover of vascular plants, covers of litter, mosses and three herb layers (the highest, the shortest and the intermediate one) as well as spider and beetle species composition and individual abundance per plot/year. We also distinguished the Carabidae family as part of the beetle community because it was the most numerous group of beetles in our collection. The procedure was carried out for vegetation and three arthropod groups separately. We took two dimensions, which described more than 55% of relative inertia, and visualised the results using the Correspondence Analysis module of the StatSoft Statistica 6.0 package.

Floristic similarity of the vegetation at the sampled plots was estimated using the Jaccard coefficient, $K_J = C / (A + B - C)$, where C = number of species registered in both plots, A = number of species at SP and B = number of species at CC (Magurran 1991). Biocoenotic similarity of the arthropod assemblages by plot/year was evaluated by the Renkonen index, $K_R = \sum \min(p_{i1}, p_{i2})$, where

p = proportion of each species in a community of N species (Jost et al. 2011).

Alpha diversity indices of the spider and beetle assemblages were calculated in the program PAST; differences between the index values were estimated by means of bootstrap analysis (Hammer et al. 2001). We chose the Shannon index of species diversity and the Pielou index of evenness to assess species richness and distribution of individuals between the species. These indices are commonly used in ecological studies including post-fire recovery of arthropod communities (Cook & Holt 2006, Freire & Motta 2011, Rose & Goebel 2015), which allows for comparison with other researches.

In terms of food preferences, we distinguished the guilds of phytophagous, zoophagous, zoo-phytophagous, necrophagous+necro-zoophagous and saprophagous insects (after Kryzhanovskiy 1983, Chernei 2005) and estimated their relative abundance for each plot/year.

Results

Vegetation characteristics

The vascular plant species lists of SP and CC were rather similar ($K_{\text{Jaccard}} = 0.59$), while the lists of SP and the other two unburnt plots, in the gully bottom and on the south-facing slope, showed considerable differences ($K_{\text{Jaccard}} = 0.31$ and 0.42 , respectively). SP was occupied by the communities of *Stipa capillata* + *Festuca valesiaca* agg. + *Bromopsis riparia* (Figure 2, background) and *Festuca valesiaca* agg. + *Bromopsis riparia* + *Pilosella officinarum*. The adjacent part of CC hosted the community of *Pilosella officinarum* + *Festuca valesiaca* agg. + *Bromopsis inermis* (Figure 2, foreground), interspersed with *Festuca valesiaca* agg. + *Bromopsis inermis* + *Pilosella officinarum* and *Bromopsis inermis* + *Festuca valesiaca* agg. Unlike in SP, *Stipa capillata* was completely absent from CC.



Figure 2: Vegetation pattern of the burnt (*Stipa capillata*, background) and unburnt (*Pilosella officinarum*, foreground) patches on the sampled slope one year after the fire, July 2015. Photo: Nina Polchaninova.

Slika 2: Vegetacija na požganih (*Stipa capillata*, v ozadju) in nepožganih (*Pilosella officinarum*, spredaj) zaplatah na vzorčenem pobočju eno leto po požaru, julij 2015. Foto: Nina Polchaninova.

In general, SP differed from CC (samples of 2014) by seven parameters out of ten (Table 1); however, there were no differences in living cover of vascular plants, cover of mosses and cover of the highest herb layer. At SP the intermediate herb layer (16 cm on average) had the highest rate of cover (30–50%, living cover 55–60%), while at CC the shortest herb layer with an average height of 3 cm was prevailing (30–45%, living cover 40–65%).

Besides the above-mentioned firm bunchgrasses, the main species that formed the herb layers at SP were *Trifolium alpestre*, *T. montanum*, *Chamaecytisus austriacus* and *Pilosella officinarum*. In late July to early August 2013, the total vegetation cover at SP varied from 80 to 98%, and the living cover of vascular plants from 55 to 60% (Table 1). The cover of litter was 25–40%, the cover of mosses 1–5%. In July 2014 the fire destroyed the living cover and most of the litter and mosses, but left half-burnt sods of grasses, coarse plant stalks and shrub stems. In the soil deep cracks were visible. Apparently, the renewal buds of bunchgrasses did not suffer much, which ensured the regrowth of vegetation triggered by the fire. The first green sprouts appeared on 7 August 2014, after the second rain (Figure 3). A week after the third rain, which fell on 18 August 2014, the mean herb height

was 7 cm, the living cover of vascular plants 5–15%. In September/October 2014, the total vegetation cover was nearly equal to the living cover, while the layer of generative sprouts was absent. Finally, in the end of the growing season, the mean vegetation height reached 20 cm and the living cover 25–40%.

One year after the fire, in July 2015, the total vegetation cover at the study plot was significantly lower than in 2013 because of the scarce cover of litter and mosses (Table 1, Table 2). The living cover of vascular plants was similar to that in the pre-fire period and increased further in 2016, the wettest year in our research (Table 1).

Dominant species composition as well as prevailing herb layers did not change at SP and CC in the post-fire period. The vegetation height was variable and reached its maximum in 2016, the three layers being always higher at SP (Table 1). The difference between SP and CC in the cover of the intermediate as well as the shortest herb layers persisted throughout the whole study period, except one layer in 2015. The fire caused a decrease in the moss and litter covers, both of which did not recover in the four following years. In total, the number of vegetation parameters that changed from the pre- to the post-fire period was much higher at SP than at CC (Table 1, Table 2).



Figure 3: Vegetation regrowth (foreground) one month after the fire, late August 2014. Photo: Vladimir Ronkin.

Figure 3: Obnova vegetacije (v ospredju) en mesec po požaru, konec avgusta 2014. Foto: Vladimir Ronkin.

Table 1: Vegetation characteristics (mean ± SD) of the study plot (SP) and conditional control (CC) in late July /early August 2013–2016 and 2018 and SP/CC pairwise comparison in the pre- and post-fire period. U-test (Mann-Whitney), N=6 for each plot per year for cover values and N=30 for vegetation height values, respectively. Statistically significant differences are highlighted in bold.

SP 13 – study plot before the fire 2013; SP14, SP15, SP16, SP18 – study plot after the fire 2014, 2015, 2016, 2018; CC14, CC15, CC16, CC18 – unburnt conditional control 2014, 2015, 2016, 2018.

Tabella 1: Značilnosti vegetacije (srednja vrednost ± SD) na raziskovalnih (SP) in kontrolni ploskvi (CC) konec julija/začetek avgusta 2013–2016 in 2018 ter primerjava parov SP/CC pred in po požaru. U-test (Mann-Whitney), N=6 za vsako ploskev vsako leto za pokrovnost in N=30 za višino vegetacije. Statistično značilne razlike so prikazane krepko.

SP 13 – raziskovalna ploskev pred požarom 2013; SP14, SP15, SP16, SP18 – raziskovalne ploskve po požaru 2014, 2015, 2016, 2018; CC14, CC15, CC16, CC18 – nepožgane kontrolne ploskve 2014, 2015, 2016, 2018.

	SP13	CC14	U	p	SP15	CC15	U	p
Total vegetation cover (%)	94.2±7.0	63.3±11.3	0.5	0.005	61.7±10.8	68.3±12.1	13.0	0.423
Living cover of vascular plants (%)	58.3±2.6	52.2±9.3	10.0	0.200	59.2±10.2	62.2±10.8	14.0	0.522
Cover of litter (%)	38.3±6.8	11.7±6.1	0.0	0.004	2.8±2.1	8.7±3.8	2.0	0.010
Cover of mosses (%)	2.8±1.8	1.6±0.9	10.5	0.230	0.1±0.1	1.8±1.1	0.0	0.004
Cover of the highest herb layer (%)	1.3±1.1	1.5±0.5	13.5	0.471	1.5±0.8	1.7±0.8	15.5	0.689
Cover of intermediate herb layer (%)	37.5±7.6	23.3±8.8	4.0	0.025	37.5±5.2	25.3±10.5	6.0	0.055
Cover of the shortest herb layer (%)	21.7±7.5	36.7±6.1	2.0	0.010	23.3±7.5	39.5±13.5	4.5	0.031
Height of the highest herb layer (cm)	53.5±5.0	38.4±10.3	93.5	<0.001	56.9±5.8	44.2±12.5	176.0	<0.001
Height of intermediate herb layer (cm)	15.7±4.0	11.5±2.5	148.0	<0.001	17.8±5.0	15.0±3.7	305.0	0.032
Height of the shortest herb layer (cm)	4.4±1.3	3.1±0.9	189.0	<0.001	4.8±1.1	2.7±1.1	96.0	<0.001

	SP16	CC16	U	p	SP18	CC18	U	p
Total vegetation cover (%)	85.0±3.2	75.0±11.0	8.5	0.128	92.2±6.5	70.8±10.2	1.0	0.006
Living cover of vascular plants (%)	83.7±2.2	70.8±8.6	4.0	0.025	71.7±7.5	65.0±7.1	9.0	0.150
Cover of litter (%)	2.7±2.0	4.3±1.0	9.0	0.150	24.2±5.8	10.8±5.8	1.5	0.008
Cover of mosses (%)	0.1±0.2	2.0±1.1	0.0	0.004	0.2±0.2	1.6±1.2	1.5	0.008
Cover of the highest herb layer (%)	2.5±1.4	2.0±0.6	15.0	0.631	3.8±3.3	1.3±0.8	4.0	0.025
Cover of intermediate herb layer (%)	52.5±7.6	25.8±7.4	0.5	0.005	50.8±10.2	26.7±12.9	2.0	0.010
Cover of the shortest herb layer (%)	30.8±8.6	40.8±3.8	5.5	0.045	21.2±6.6	40.0±12.6	3.0	0.016
Height of the highest herb layer (cm)	75.8±10.6	46.8±14.2	20.0	<0.001	60.2±10.7	45.6±13.5	168.0	<0.001
Height of intermediate herb layer (cm)	30.7±5.8	17.5±3.7	15.5	<0.001	27.6±9.9	14.3±3.9	90.5	<0.001
Height of the shortest herb layer (cm)	6.0±1.6	3.8±1.2	111.0	<0.001	5.9±1.8	2.8±1.1	66.5	<0.001

Table 2: Results of the pairwise comparison (U-test, Mann-Whitney) of vegetation characteristics of the study plot (SP) and conditional control (CC), depending on the time since the fire event. Data collected late July/early August 2013–2016 and 2018. Statistically significant differences are highlighted in bold. For abbreviations see Table 1.

Table 2: Rezultati parnih primerjav (U-test, Mann-Whitney) značilnosti vegetacije na raziskovalnih (SP) in kontrolnih ploskvah (CC) v odvisnosti od preteklega časa od požara. Podatki so bili zbrani konec julija/začetek avgusta 2013–2016 in 2018. Statistično značilne razlike so prikazane krepko. Za okrajšave glej Tabelo 1.

	SP13/SP15		SP13/SP16		SP13/SP18		CC14/CC15		CC14/CC16		CC14/CC18	
	U	p	U	p	U	p	U	p	U	p	U	p
Total vegetation cover (%)	0.0	0.004	5.5	0.045	11.0	0.262	13.0	0.423	8.0	0.109	11.5	0.298
Living cover of vascular plants (%)	12.0	0.337	0.0	0.004	2.0	0.010	8.0	0.109	2.0	0.010	4.5	0.031
Cover of litter (%)	0.0	0.004	0.0	0.004	2.0	0.010	13.0	0.423	4.0	0.025	16.5	0.810
Cover of mosses (%)	0.0	0.004	0.0	0.004	0.0	0.004	16.5	0.810	13.5	0.471	16.5	0.810
Cover of the highest herb layer (%)	14.0	0.522	8.0	0.109	6.0	0.055	16.5	0.810	10.5	0.230	13.5	0.471
Cover of intermediate herb layer (%)	17.0	0.873	3.0	0.016	5.0	0.037	17.0	0.873	12.0	0.337	15.0	0.631
Cover of the shortest herb layer (%)	16.5	0.810	7.5	0.093	17.5	0.936	17.5	0.936	10.5	0.230	14.5	0.575
Height of the highest herb layer (cm)	306.5	0.034	2.5	<0.001	298.0	0.025	326.5	0.068	312.5	0.042	308.0	0.036
Height of intermediate herb layer (cm)	344.0	0.117	8.5	<0.001	133.0	<0.001	187.0	<0.001	106.5	<0.001	213.5	<0.001
Height of the shortest herb layer (cm)	366.0	0.214	198.5	<0.001	221.5	0.001	349.0	0.135	304.5	0.031	349.0	0.135

CA ordination of SP and CC based on vegetation characteristics is shown on Figure 4. The position of SP13 on both axes reflects its maximal difference from the other plots/years. In 2015–2016, SP and CC became closer on the first axis, but more distant on the second one. In general, the ordination shows the difference between CC and SP and its change in time after the fire. Relative inertia by the dimension 1 was maximal for the cover of litter (0.76) and the cover of the shortest herb layer (0.14). The dots representing these characteristics have the largest distance along Axis 1 (Fig. 4, dots 3 and 7, respectively). The cover of the intermediate herb layer (0.41), the cover of the shortest herb layer (0.39) and the cover of mosses (0.13) had the highest inertia by the dimension 2. The two dots corresponding to the cover of the intermediate herb layer (Figure 4, dot 6) and the cover of mosses (Figure 4, dot 4) are the most distant on Axis 2.

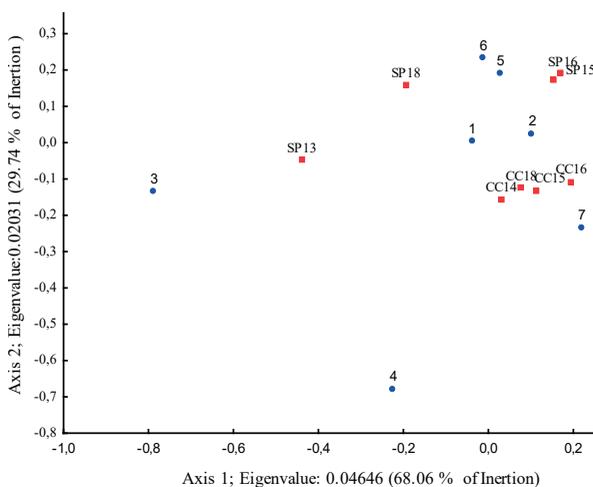


Figure 4: CA ordination of the burnt (SP) and unburnt (CC) plots in 2013–2016 and 2018 based on vegetation characteristics: total vegetation cover (1), living cover of vascular plants (2), cover of litter (3), cover of mosses (4) and cover of three herb layers (the highest (5), the intermediate (6) and the shortest (7)). For abbreviations see Table 1.
Slika 4: Ordinacija CA požganih (SP) in nepožganih (CC) ploskev v letih 2013–2016 in 2018 na podlagi značilnosti vegetacije: skupna pokrovnost vegetacije (1), pokrovnost živih rastlin (2), pokrovnost opada (3), pokrovnost mahov (4) in pokrovnost treh plasti zelišč (najvišje (5), srednje (6) in najnižje (7)). Za okrajšave glej Tabelo 1.

Arthropod assemblages Spiders

Spider assemblages were represented by only 13 species from five families; of these, six species belonged to the family Lycosidae (Appendix, Table 1). The number of species per plot and year ranged from six to nine. Species diversity (Shannon index) did not change at the newly burnt plot (SP13 vs SP14), then grew in the following

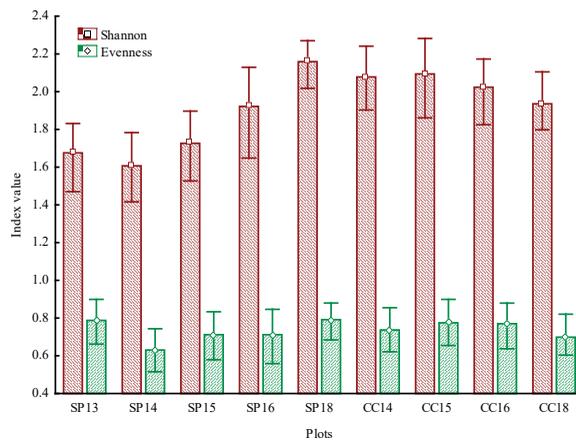


Figure 5: Alpha diversity indices of spider assemblages at the burnt (SP) and unburnt (CC) plots depending on the time since the fire event. Data collected yearly in September/October 2013–2016 and 2018. Whiskers indicate min and max bootstrap values. For abbreviations see Table 1.
Slika 5: Indeksi alfa diverzitete združb pajkov na požganih (SP) in nepožganih (CC) ploskvah v odvisnosti od preteklega časa od nastanka požara. Vzorce smo zbirali vsako leto septembra/oktobra v letih 2013–2016 in 2018. Brki na grafih prikazujejo minimalne in maksimalne vrednosti, ki smo jih dobili z metodo ponovnega vzorčenja (bootstrap). Za okrajšave glej Tabelo 1.

years and reached a statistically significant difference only in 2018 (Figure 5). Species diversity at CC fluctuated in narrower ranges than at SP and differed significantly compared to SP13 and SP14. The evenness of the spider assemblages during the study period was constant, with one statistically not significant drop after the fire (SP14). Spider activity density varied only insignificantly over the years at both plots except at CC in 2016 (Figure 6, Kruskal-Wallis test: $H = 9.445$, $df = 6$, $P = 0.150$).

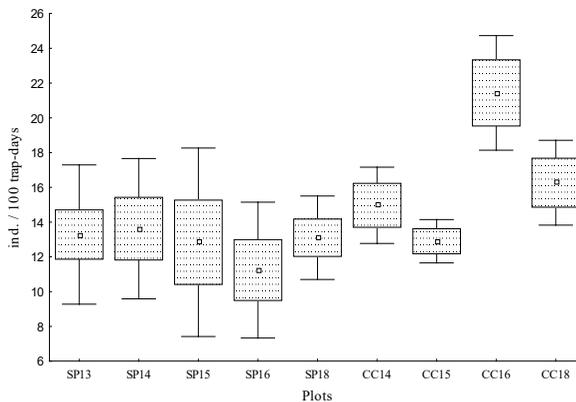


Figure 6: Average activity density of spiders at the burnt (SP) and unburnt (CC) plots in September/October 2013–2016 and 2018 (dots – mean value, boxes – standard error, whiskers – standard deviation). For abbreviations see Table 1.
Slika 6: Povprečna gostota aktivnosti pajkov na požganih (SP) in nepožganih (CC) ploskvah septembra/oktobra v letih 2013–2016 in 2018 (točka – srednja vrednost, škatle – standardna napaka, brki – standardni odklon). Za okrajšave glej Tabelo 1.

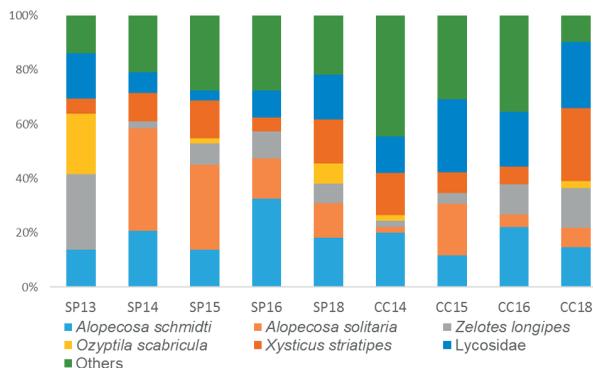


Figure 7: Dominance structure of spider assemblages at the burnt (SP) and unburnt (CC) plots in September/October 2013–2016 and 2018. For abbreviations see Table 1.

Slika 7: Struktura dominance v združbah pajkov na požganih (SP) in nepožganih (CC) ploskvah septembra/oktobra v letih 2013–2016 in 2018. Za okrajšave glej Tabela 1.

Two lycosids, *Alopecosa schmidti* and *A. solitaria*, were the most abundant spider species in our collection (20.57% and 17.9% of individuals, respectively). *A. solitaria* appeared at the study plot after the fire and peaked in the first two years (Figure 7). The number of *A. schmidti* varied by plots and years. The dynamics of its peaks and lows coincided at both SP and CC. Before the fire the study plot was dominated by other species, *Ozyptila scabricula* and *Zelotes longipes*. They were absent or not numerous at both plots in the post-fire period, except in 2016 and 2018, when *Z. longipes* was more abundant at CC (Figure 7). Juvenile lycosids were present at both plots being less numerous at SP in 2014–2016. In 2018 their relative abundance reached the level of 2013 (16.4% vs 17.6%, respectively). During the study period *Xysticus striatipes* demonstrated only one peak of abundance, which changed the spider dominance structure at CC in 2018 (Figure 7).

CA separates the study plot in 2013, confirming the difference of the pre-fire spider assemblage. Post-fire SP14

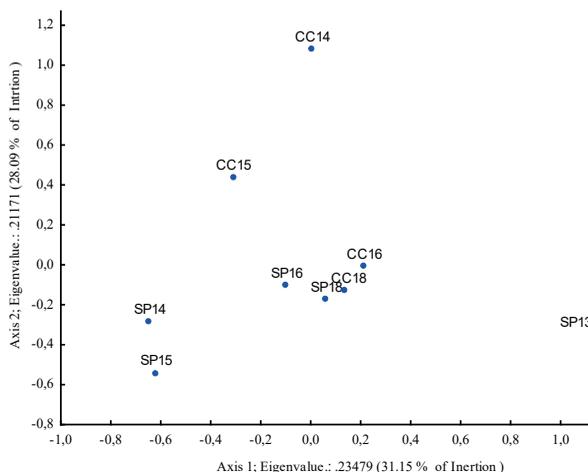


Figure 8: CA ordination of the burnt (SP) and unburnt (CC) plots in 2013–2016 and 2018 based on spider species composition and dynamic density. For abbreviations see Table 1.

Slika 8: Ordinacija CA požganih (SP) in nepožganih (CC) ploskev na osnovi vrstne sestave pajkov in dinamične gostote. Za okrajšave glej Tabela 1.

and SP15 stand at the opposite side of the first ordination axis, while the other dots of plots/years occupy intermediate positions. Remarkable is the proximity of SP and CC in 2016 and 2018 on both axes. The ordination shows that the recently burnt SP14 was most distant from both CC14 and SP13 (Figure 8). Biocoenotic similarity indices of the compared spider assemblages (K_R , Tab 3) correspond to the CA results. The lowest was the similarity in the pairs SP13 – SP14 and SP13 – SP15 (0.365 and 0.381), and the highest in the pair SP14 – SP15 (0.728). At SP the index grew with time to 0.551 (SP13 – SP18), while at CC it ranged from 0.589 to 0.634, showing smaller variations. The pairwise similarity between the burn/unburnt plots was minimal in 2014 (0.558) and maximal in 2016 (0.757). In the latter case the difference between the plots was statistically insignificant ($P > 0.05$, Table 3).

Table 3: Biocoenotic similarity (Renkonen index K_R) of the spider (left bottom triangle) and beetle (right top triangle) assemblages by plot/year in 2013–2016 and 2018. For abbreviations see Table 1

Table 3: Biocenotska podobnost (Renkonen indeks K_R) združb pajkov (leva spodnja polovica) in hroščev (desna zgornja polovica) na ploskvah v letih 2013–2016 in 2018. Za okrajšave glej Tabela 1.

	SP13	SP14	SP15	SP16	SP18	CC14	CC15	CC16	CC18	
SP13		0.373	0.265	0.394	0.245	0.337	0.318	0.317	0.248	
SP14	0.381		0.525	0.693	0.460	0.711	0.636	0.726	0.609	
SP15	0.365	0.728		0.540	0.502	0.466	0.721	0.459	0.602	
SP16	0.498	0.674	0.532		0.561	0.503	0.582	0.562	0.642	
SP18	0.551	0.603	0.641	0.655		0.319	0.481	0.363	0.681	
CC14	0.481	0.588	0.440	0.561	0.634		0.552	0.710	0.504	P < 0.001
CC15	0.428	0.582	0.507	0.613	0.655	0.589		0.593	0.672	P < 0.01
CC16	0.590	0.583	0.438	0.757	0.688	0.634	0.626		0.585	P < 0.05
CC18	0.577	0.490	0.585	0.531	0.686	0.601	0.597	0.671		P > 0.05

Insects

The autumnal beetle assemblages were comprised of 61 taxa (54 identified to the species level). Species richness was the lowest at SP14 and CC18 (11 taxa each) and the highest at CC14 (28 taxa). In the other cases it varied from 16 to 21 taxa per plot and year (Appendix, Table 2). In total, 37 beetle taxa were recorded at the study plot (21 taxa in the pre-fire year 2013 and 33 taxa in the four post-fire years) and 47 taxa at the conditional control. The Shannon index dropped at SP right after the fire, but recovered in the following year. All in all it varied insignificantly at both plots except CC18 (Figure 9). The evenness was low only in one case, namely at CC14 due to the predominance of the ground beetle *Calathus fuscipes*. This species was dominant at both plots except SP in 2013 and 2018, but in the other years it was accompanied with higher numbers of second-rank dominants like *Calathus ambiguus*, *Dermestes lanarius*, *Ophonus stictus*, *Cryptophagus* sp. and Staphilinidae spp. (Figure 10). In 2018 the two *Calathus* species reversed their dominance positions, *C. ambiguus* now being prevalent at SP. Before the fire the study plot was dominated by *Galeruca pomonae*. In contrast, *Zabrus spinipes* appeared at the fire site in 2014 and increased its number of individuals during our study.

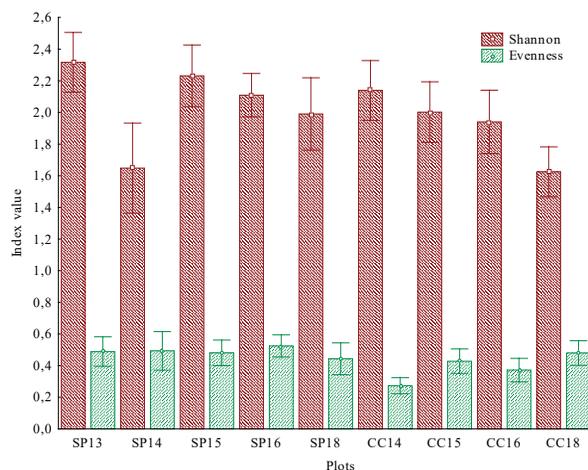


Figure 9: Alpha diversity indices of beetle assemblages at the burnt (SP) and unburnt (CC) plots depending on the time since the fire event. Data collected yearly in September/October 2013–2016 and 2018. Whiskers indicate min and max bootstrap values. For abbreviations see Table 1.

Slika 9: Indeksi alfa diverzitete združb hroščev na požganih (SP) in nepožganih (CC) ploskvah v odvisnosti od preteklega časa od nastanka požara. Vzorci smo zbirali vsako leto septembra/oktobra v letih 2013–2016 in 2018. Brki na grafih prikazujejo minimalne in maksimalne vrednosti, ki smo jih dobili z metodo ponovnega vzorčenja (bootstrap). Za okrajšave glej Tabelo 1.

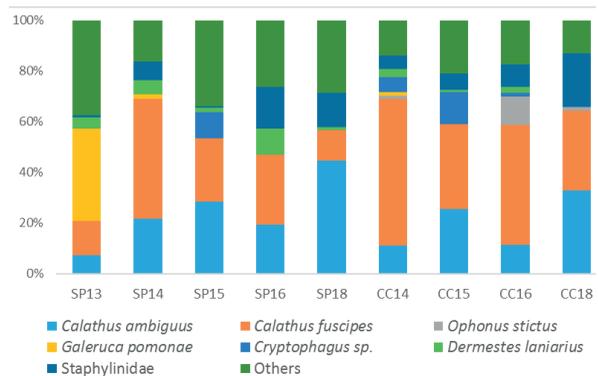


Figure 10: Dominance structure of beetle assemblages at the burnt (SP) and unburnt (CC) plots in September/October 2013–2016 and 2018. For abbreviations see Table 1.

Slika 10: Struktura dominanc v združbah hroščev na požganih (SP) in nepožganih (CC) ploskvah septembra/oktobra v letih 2013–2016 in 2018. Za okrajšave glej Tabelo 1.

Beetle activity density did not differ significantly by plots/years (Kruskal-Wallis test: $H = 7.420$, $df = 6$, $P = 0.284$). Still, on average it was slightly higher and varied in a wider range at the conditional control (Figure 11). CA ordination based on the structure of beetle assemblages distinguishes SP13 on Axis 1. The other plots/years show the differences only on Axis 2, SP and CC being closest in 2014 (Figure 12 A). An analysis of the ground beetle assemblages gives another ordination of the sampled plots in the study years (Figure 12 B). SP13 stands apart only on Axis 2, while SP18 is most separated along both axes.

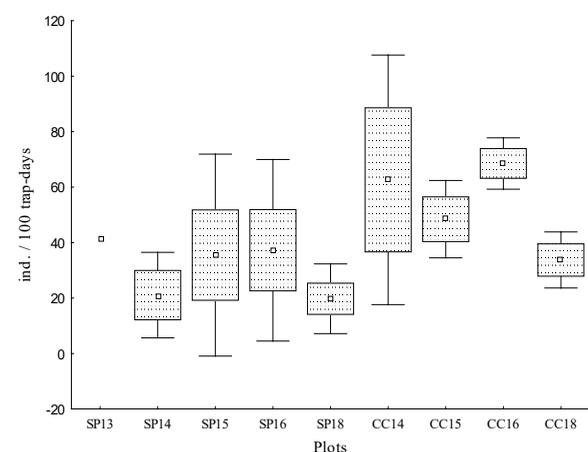


Figure 11: Average activity density of beetles at the burnt (SP) and unburnt (CC) plots in September/October 2013–2016 and 2018 (dots – mean value, boxes – standard error, whiskers – standard deviation). For abbreviations see Table 1.

Slika 11: Povprečna gostota aktivnosti hroščev na požganih (SP) in nepožganih (CC) ploskvah septembra/oktobra v letih 2013–2016 in 2018 (točka – srednja vrednost, škatle – standardna napaka, brki – standardni odklon). Za okrajšave glej Tabelo 1.

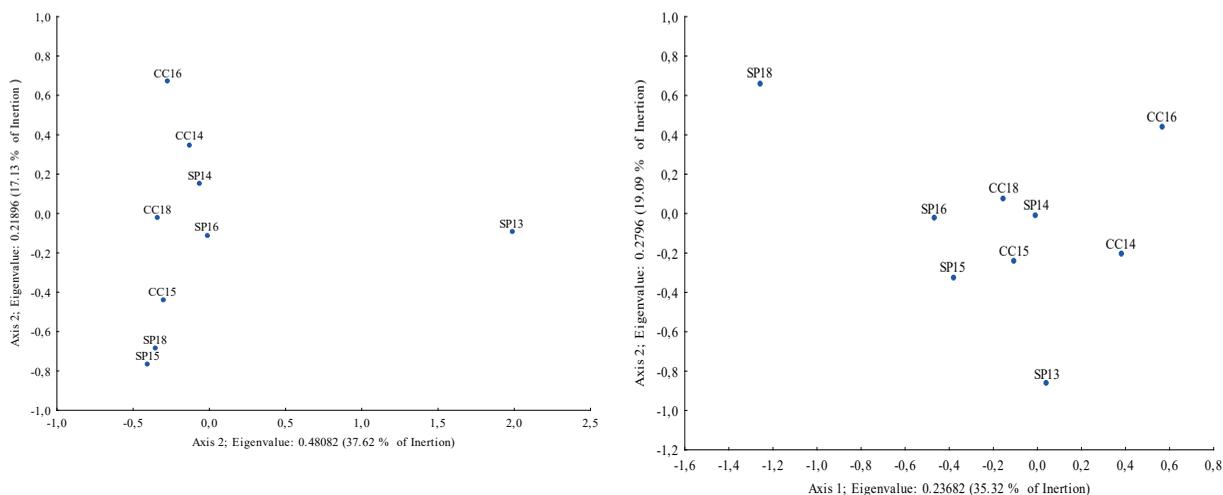


Figure 12: CA ordination of the burnt (SP) and unburnt (CC) plots in 2013–2016 and 2018 based on beetle species composition and dynamic density. A – beetles in total, B – ground beetles (Carabidae). For abbreviations see Table 1.

Slika 12: Ordinacija CA požganih (SP) in nepožganih (CC) ploskev v letih 2013–2016 in 2018 na podlagi vrstne sestave hroščev in dinamične gostote. A – hrošči skupaj, B – krešiči (Carabidae). Za okrajšave glej Tabelo 1.

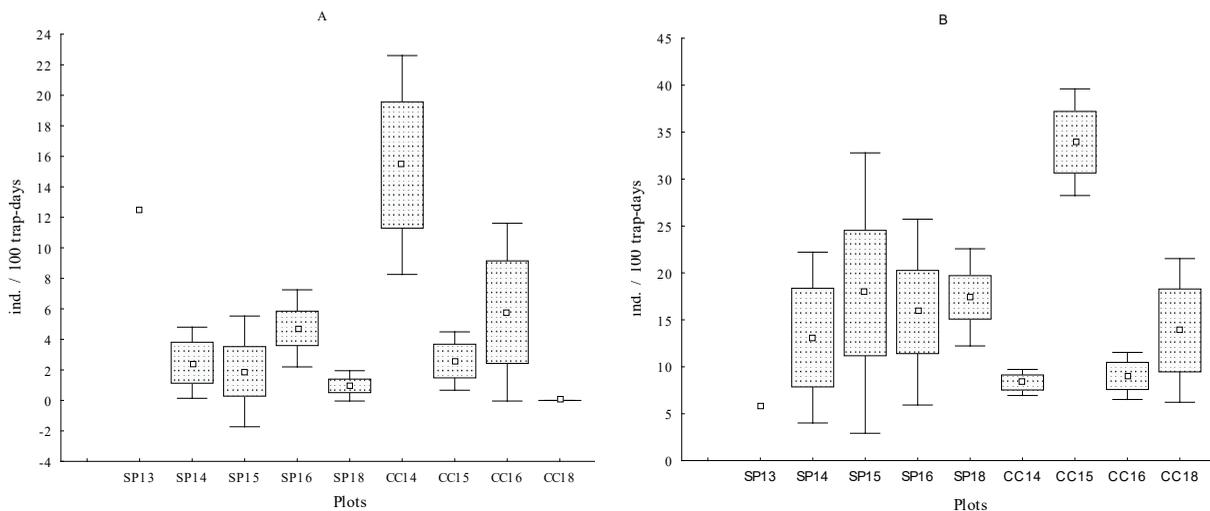


Figure 13: Average activity density of leafhoppers (Cicadinea) (A) and acridids (Acridoidea) (B) at the burnt (SP) and unburnt (CC) plots in September/October 2013–2016 and 2018 (dots – mean value, boxes – standard error, whiskers – standard deviation). For abbreviations see Table 1.

Slika 13: Povprečna gostota aktivnosti škržatov (Cicadinea) (A) in poljskih kobilic (Acridoidea) na požganih (SP) in nepožganih (CC) ploskvah septembra/oktobra v letih 2013–2016 in 2018 (točka – srednja vrednost, škatle – standardna napaka, brki – standardni odklon). Za okrajšave glej Tabelo 1.

The similarity index of the beetle assemblages was the lowest when comparing SP13 with the other plots/years (Table 3). It had no clear trend in time since fire, ranging from 0.245 to 0.394 at SP and from 0.504 to 0.710 at CC. The pairwise comparison showed higher similarity of the two plots in the first and the second post-fire years (0.711 and 0.721).

The leafhoppers' dynamic density decreased after the fire and remained low during the whole study period (Figure 13 A). At CC their annual abundance was highly variable with a peak in 2014 and the absence in samples in 2018. In contrast, the acridids showed an increase in numbers at the fire site and again a high fluctuation of their activity density at CC (Figure 13 B).

Trophic guilds

The insect assemblage of the pre-fire SP differed from the others by the highest rate of phytophages and the lowest of zoophages (Figure 14). Right after the fire there were no saprophagous insects at the fire site, but they re-appeared the next year in an even higher proportion than at the conditional control. In total, an increased share of phyto-zoophages made the trophic structure of insect assemblages at the post-fire SP similar to that at CC. The ratio of phytophages grew at SP only in 2018, but was then still lower than in 2013.

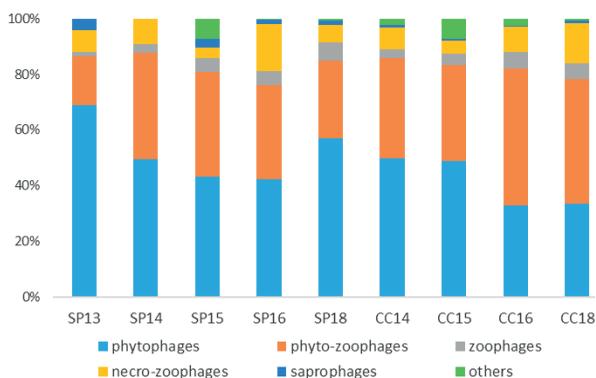


Figure 14: Trophic guilds of the insects at the burnt (SP) and unburnt (CC) plots in September/October 2013–2016 and 2018. For abbreviations see Table 1.

Slika 14: Prehramnevalne združbe žuželk na požganih (SP) in nepožganih (CC) ploskvah septembra/oktobra v letih 2013–2016 in 2018. Za okrajšave glej Tabelo 1.

Discussion

Rolling topography as well as uneven grazing pressure and various terms of grazing cessation have created a vegetation pattern in the study site (Ronkin & Savchenko 2016). The abandoned pastures host a variety of vegetation assemblages at different stages of the post-grazing succession. The herbage differs by height and plant biomass, which shapes a patchy blanket of more or less flammable material. In such conditions wildfires destroy the whole vegetation at some places and leave others intact, creating natural refuges for the steppe inhabitants, which later become a source of recolonisation.

The vegetation of SP can be characterised as a community of *Stipa capillata* + *Festuca valesiaca* agg. with a successional trend toward the dominance of grasses. The cover of the highest herb layer formed by the feather grass increased threefold during the study period (Table 1). By the time of the fire, the plants had completed their seasonal growth, and the herbage was dried up. Moreover,

the plot had accumulated a lot of litter, since grazing had long been ceased, and had become highly flammable. The vegetation of the adjacent plots was still in its growth period or had sparse structures with shallow litter, which saved it from burning.

The two plot types SP and CC differed visually (Figure 2). The Correspondence Analysis conducted in our study highlighted the main vegetation parameters responsible for this difference. Based on the maximal distance of the dots “cover of litter” and “cover of the shortest herb layer” (Figure 4, dots 3 and 7, respectively) along Axis 1, we can interpret the latter as an axis of the main differences between the vegetation characteristics of the pre-fire SP (SP13) and any research year of CC. Thus, the position of the dot SP13 was determined by the high level of the cover of litter (Table 1), which was the main distinguishing feature of this plot. In the post-fire years SP and CC became similar in the cover of litter and in the cover of the shortest herb layer as illustrated by the strong convergence between the dots SP15 and SP16 and all the dots of CC along Axis 1. Only in 2018 litter accumulation resulted in the approximation of the pre- and post-fire SP, which is reflected in the graph by the intermediate position of SP18 between SP13 and all the other dots. Presumably, the slow recovery of the cover of litter can be explained by the extremely wet conditions in 2016, which promoted accelerated litter decomposition. Axis 2 can be interpreted as an axis of differences in the traits of post-fire SP and CC. This axis reflects the cover of the intermediate herb layer and the cover of mosses. The cover of mosses at the pre-fire SP was closer to that at CC and did not recover in the four-year period.

Many authors (Cook & Holt 2006, Engle et al. 2008, Doxon et al. 2011) highlighted the importance of refuges for successful post-burn recovery, but the attributes that determine the refuges’ value and the ways of animal migrations are still poorly known (Robinson et al. 2013). Colonisation does not necessarily occur from the nearest unburnt areas, but from the underground (carabid beetles) or from long distances (Cook & Holt 2006).

The first question of our study was what arthropods are the first to colonise the fire site. These were mobile spiders and insects common in the study area (Polchaninova et al. 2016a). *Alopecosa solitaria* was the only species that clearly benefited from the fire: It dominated the burnt site two consecutive years, being less abundant at the unburnt plot. Six out of thirteen collected spider species are typical dry grassland dwellers with autumnal breeding periods. Nearly all of them are good runners and occur widely on steppe slopes (personal observations). Two dominant beetles (*Calathus ambiguus* and *C. fuscipes*) were common for both plots; the former was particularly numerous in 2018

and the latter in 2014. They are polyphagous habitat generalists with a high dispersal capacity, often found in natural and ruderal vegetation. The periodical dominants of the investigated plots, *Ophonus stictus* (phytophagous) and *Dermestes laniarius* (necrophagous), are widely distributed in dry grasslands. The other beetle species were found as singletons at the study plot shortly after the fire, and more than half of them belonged to carabids.

These results are consistent with other studies, which report the absence of pyrophyllous arthropod species at burnt steppe sites (Samu et al. 2010, Polchaninova et al. 2016b) and their colonisation by mobile species from unburnt areas in close proximity (Savchenko 2009, Prokopenko & Savchenko 2013, Rose & Goebel 2015, Valkó et al. 2016).

If considering species diversity (estimated by the index values) and average activity density, only minor changes can be observed between the pre- and the post-fire period. Beetle diversity dropped after the fire, but then recovered, spider evenness decreased insignificantly, and activity density of both groups varied in a narrow range. The absence of a decline in diversity and abundance may be explained by surviving or colonisation (Rose & Goebel 2015). In our study the only trend was seen in the gradual increase in spider species diversity, which reached its maximum in the fourth year after the fire.

The second question was how the arthropod assemblages have changed between pre- and post-fire period. The differences were manifested in the assemblage structure, namely dominant complexes and trophic guild ratio. The changes in dominant complexes could have resulted from an alteration of vegetation assemblages, which, in turn, altered microclimatic conditions and food resources. Although variable in the number of species, the post-fire beetle assemblages of the burnt and unburnt plots were more similar to each other than to the pre-fire assemblages. Presumably, the vegetation change in favour of grasses caused a decrease in the number of *Galeruca pomonae* (a phytophagous species feeding on various forbs (Koch 1992)) and an increase in *Zabrus spinipes* (a granivorous species). If we consider the ground beetles separately, as the largest systematic and ecologically uniform group in our collection, the pre- and post-fire differences were less pronounced. On the other hand, annual changes in carabid assemblages were clearly seen. For example, the high abundance of *Calathus fuscipes* at the unburnt plot in 2014 and 2016 and an increase in the number of *C. amdiguus* at the burnt plot in 2018 cannot be explained by the impact of fire.

Spiders showed higher sensitivity to the changing microclimatic conditions, which made it possible to distinguish three assemblage groups: pre-fire, early post-fire (1–12 months) and late post-fire (24–48 months). The third group was very close to the assemblages at the un-

burnt plot intact by the fire. Moreover, it tended to converge with the pre-fire assemblage at the study plot.

Spiders and beetles often display different responses to the same disturbance factor in various fire-prone landscapes (Pryke & Samways 2012). Studies of the arthropod post-fire recovery in European dry grasslands revealed a simplified structure and higher abundance of beetle assemblages, but no quantitative/qualitative changes in spiders (Samu et al. 2010, Hungarian Plain), as well as contrasting trajectories of their assemblage traits in the bunchgrass steppes (Prishutova & Arzanov 2008) and meadow steppes (Polchaninova et al. 2016b, Russian Plain). However, other studies showed neutral reaction of both groups (Valkó et al. 2016). In our case two spider and one beetle species increased in number of individuals after the fire, one beetle species decreased, the others remained neutral or followed annual changes. At the assemblage level, the similarity between spiders before and after the fire increased gradually, while the beetles did not show any tendencies.

The acridids benefited from the fire and increased in numbers, while the leafhoppers, in contrast, responded negatively. A short post-fire increase in density or biomass was observed in burnt tallgrass prairies for Acrididae (Meyer et al. 2002, Joern 2004), and no effect was reported for Cicadellidae (Hartley et al. 2007).

Trophic group ratio can also serve as indicator of the effect of fire on arthropod communities (Kral et al. 2017). The influence can be traced across all trophic levels and depends, like the other traits of the arthropod assemblages, on many factors. In general, food specialists are less successful than generalists in disturbed areas (Cook & Holt 2006, Vogel & Kofard 2010). In some cases phytophages that feed on grasses (Meyer et al. 2002) or have a granivore strategy (Samu et al. 2010) are favored by fire, in other cases forb-feeders (Meyer et al. 2002, Joern 2004) are more successful. Predators with a wide diet spectrum have also reported to be more abundant at the fire sites (Cook & Holt 2006, New 2015).

In the course of our study, we observed a decrease of phytophages, an increase of omnivores and the absence of saprophages in the year of the fire event. The saprophages recovered easily with the accumulation of dead plant material, while the phytophages' proportion remained low for two post-fire years and tended to recover only in 2018.

In all the studied groups, the four-year fluctuations of species richness and/or individual abundance was higher at the unburnt plot. Such a phenomenon was also observed in North-American grasslands (Rose & Goebel 2015). The undisturbed sites developed in accordance to their annual cycles, which was disrupted by fire in the burnt areas. Consequently, it triggered recovery processes, which can follow different routes.

Predicting the development of post-fire arthropod communities is challenging (Koltz et al. 2018). In some cases of small-scale prescribed burning, they recover in a year despite the obvious changes in vegetation structure (Valkó et al. 2016), in other cases in two or three years (Wade & Roughley 2010, Pryke & Samways 2012). Differences between the arthropod abundance, diversity or even assemblage structures at the burnt and unburnt sites can diminish in one to two years (Savchenko 2009, Prokopenko & Savchenko 2013, Polchaninova et al. 2016b) or, in vulnerable groups, last much longer (Swengel 2001, Panzer 2002, New 2015). According to Collins (2000), the post-fire recovery depends on community stability. Stable communities can vary more from one year to the next, yet follow their general temporal trajectory (Collins 2000). They resist disturbance and are capable of rapid recovery (Holling 1973).

Given the considerable successional changes in vegetation, the post-grazing ecosystems in Ukraine are highly unstable (Tkachenko 2009). A number of driving factors (frequency of burning, burnt area, season, intensity, weather conditions) influence the direction of the post-fire vegetation recovery, which creates an even finer mosaic of plant communities at various successional stages (Tkachenko et al. 2010). We can hypothesise that in our case study the small-scale fire destroyed the patchiness of the arthropod community and changed the trajectory of its post-grazing succession. In case of a large-scale fire, the whole mosaic would have been lost. We consider that prescribed burning in Ukrainian gully steppes should be applied only at a very small scale as a prevention measure of extensive wild fires. We recommend fine-scale patch-burning in late autumn when mosses and litter still keep their moisture and the season of invertebrate activity is over.

Conclusion

A patched summer fire had a long-term effect on steppe vegetation and cursorial arthropods. The living cover of vascular plants recovered in the year after the fire, while the cover of mosses and litter did not recover within four years. The burnt plot was colonised by mobile arthropods occurring in the grassland habitats of the study area. The differences in spider and insect species diversity and/or abundance at the burnt/unburnt plots were not pronounced. The disturbance became manifest in the assemblage structures, in particular in dominant complexes and trophic guilds, making them more or less similar to those of the unburnt plot. In terms of ecological diversity, the fire reduced differences between the arthropod assemblages hosted by two adjacent plots distinguished by vegetation

parameters. Our investigations revealed the variety of the arthropod response to fire disturbance at the species/group level. The spider assemblages showed a tendency to recover to the pre-fire state, while the beetle assemblages retained significant differences during the whole study period.

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Appendix

Table 1: Spider species composition and number of individuals at the sampled plots before and after the fire. Data collected yearly September/October 2013–2016 and 2018. SP13 – study plot before the fire event 2013; SP14, SP15, SP16, SP18 – study plot after the fire 2014, 2015, 2016, 2018; CC14, CC15, CC16, CC18 – unburnt conditional control 2014, 2015, 2016, 2018.

Tabela 1: Vrsta sestava in število osebkov pajkov na vzorčnih ploskvah pred in po požaru. Podatke smo zbirali vsako leto septembra/oktobra v letih 2013–2016 in 2018. SP13 – raziskovalna ploskev pred požarom 2013; SP14, SP15, SP16, SP18 – raziskovalne ploskve 2014, 2015, 2016, 2018; CC14, CC15, CC16, CC18 – nepožgane kontrolne ploskve 2014, 2015, 2016, 2018.

Species	Study plot / Conditional control								
	SP13	SP14	SP15	SP16	SP18	CC14	CC15	CC16	CC18
<i>Eresus kollari</i> Rossi, 1846	·	1	6	1	3	·	1	1	1
<i>Alopeosa schmidti</i> (Hahn, 1835)	5	16	7	13	10	9	3	10	6
<i>A. solitaria</i> (Herman, 1879)	·	29	16	6	7	1	5	2	3
<i>A. taeniopus</i> (Kulczyński, 1895)	·	·	·	·	·	3	1	·	·
<i>Trochosa robusta</i> (Simon, 1876)	2	5	·	3	1	3	1	4	1
<i>T. ruricola</i> (De Geer, 1778)	·	·	·	1	·	·	1	·	·
<i>Xerolycosa miniata</i> (C. L. Koch, 1834)	·	·	·	·	·	4	2	·	·
Lycosidae spp. juv.	6	6	2	4	9	6	7	9	10
<i>Cheiracanthium</i> sp. juv.	·	·	·	·	·	·	·	1	1
<i>Gnaphosa licenti</i> Schenkel, 1953	·	·	·	·	·	1	·	·	·
<i>G. lugubris</i> (C. L. Koch, 1839)	·	·	·	·	2	·	·	·	·
<i>Zelotes longipes</i> (L. Koch, 1866)	10	2	4	4	4	1	1	5	6
Gnaphosidae spp. juv.	·	2	·	2	5	1	2	4	·
<i>Ozyptila scabricula</i> (Westring, 1851)	8	·	1	·	4	1	·	·	1
<i>Xysticus striatipes</i> L. Koch, 1870	2	8	7	2	9	7	2	3	11
Thomisidae sp. juv.	·	·	1	·	·	·	·	·	1
<i>Aelurillus v-insignitus</i> (Clerck, 1757)	1	·	·	2	1	·	·	3	·
Total taxa (species)	7 (6)	9(7)	9(6)	10(8)	11(9)	11(9)	11(9)	11(8)	10(7)
Total individuals	34	69	44	38	55	37	26	42	41

Table 2: Insect species composition and number of individuals at the sampled plots before and after the fire. Data collected yearly September/October 2013–2016 and 2018. For abbreviations see Tab. 1. Trophic groups: phyt – phytophages, zoo – zoophages, zoo-phyt – zoo-phytophages, necr – necrophages, sapr – saprophages, mycet – mycetophages, copr – coprophages.

Tabela 2: Vrstna sestava in število osebkov žuželk na vzorčnih ploskvah pred in po požaru. Podatke smo zbirali vsako leto septembra/oktobra v letih 2013–2016 in 2018. Za okrajšave glej Tabela 1. Trofične skupine: phyt – fitofagi, zoo – zoofagi, zoo-phyt – zoo-phytofagi, necr – nekrofagi, sapr – saprofagi, mycet – micetofagi, copr – koprofagi.

Family	Species	Trophic group	Study plot / Conditional control												
			SP13	SP14	SP15	SP16	SP18	CC14	CC15	CC16	CC18				
Coleoptera															
Brentidae	Apioninae	phyt
Byrrhyidae	<i>Porcinolus murinus</i> (Fabricius, 1794)	phyt	1	1
Carabidae	<i>Anara crenata</i> Dejean, 1828	phyt	1
Carabidae	<i>Anara equestris</i> (Dufschmid, 1812)	phyt	1
Carabidae	<i>Anara ingenua</i> (Dufschmid, 1812)	phyt	1
Carabidae	<i>Anara litorea</i> C.G. Thomson, 1857	zoo-phyt	1
Carabidae	<i>Anisodactylus binotatus</i> (Fabricius, 1787)	zoo-phyt	1
Carabidae	<i>Anisodactylus signatus</i> (Panzer, 1796)	zoo-phyt	1	1
Carabidae	<i>Bruchinus crepitans</i> (Linnaeus, 1758)	zoo	1
Carabidae	<i>Calathus ambiguus</i> (Paykull, 1790)	zoo-phyt	8	12	38	26	26	37	17	17	28	15	28	15	28
Carabidae	<i>Calathus fuscipes</i> (Goeze, 1777)	zoo-phyt	15	26	33	37	37	10	90	90	37	63	27	63	27
Carabidae	<i>Calathus melanocephalus</i> (Linnaeus, 1758)	zoo-phyt	1	.	4	1	1
Carabidae	<i>Chlaenius aeneocephalus</i> Dejean, 1826	zoo	1
Carabidae	<i>Gymnoidis angularis</i> (Gyllenhal, 1810)	zoo	4	.	.	.	1	1	1	1
Carabidae	<i>Gymnoidis scapularis</i> Schaum, 1857	zoo	.	1	3	1	1
Carabidae	<i>Dinodes decipiens</i> (L. Dufour, 1820)	zoo	.	1	2	.	.	.
Carabidae	<i>Harpalus caspius</i> (Steven, 1806)	phyt	2	.	.	1
Carabidae	<i>Harpalus distinguendus</i> Dufschmid, 1812	phyt	.	.	2	.	1	.	.	.	1
Carabidae	<i>Harpalus rubripes</i> (Dufschmid, 1812)	phyt	.	.	.	1	1	1
Carabidae	<i>Harpalus rufipes</i> DeGeer, 1774	phyt	1
Carabidae	<i>Harpalus subcylindricus</i> Dejean, 1829	phyt	1	1
Carabidae	<i>Notiophilus laticollis</i> Chaudoir, 1850	zoo	1	.	7	.	1	1	2	4	2	5	5	5	5
Carabidae	<i>Ophonus azureus</i> (Fabricius, 1775)	phyt	.	.	6	.	1	1	2	4
Carabidae	<i>Ophonus rufibarbis</i> (Fabricius, 1792)	phyt	1
Carabidae	<i>Ophonus stictus</i> Stephens, 1828	phyt	2	.	.	15	1	15	1
Carabidae	<i>Poecilus koyi</i> (Germar, 1823) (= <i>sericeus</i> Fischer von Waldheim, 1824)	zoo	.	1	.	.	2	4
Carabidae	<i>Poecilus punctulatus</i> (Schaller, 1783)	zoo	1
Carabidae	<i>Zabrus spinipes</i> (Fischer von Waldheim, 1817)	phyt	.	1	6	9	5

Family	Species	Study plot / Conditional control										
		SP13	SP14	SP15	SP16	SP18	CC14	CC15	CC16	CC18		
Chrysomelidae	Alicinae	4	.	1	2	.	1	7	3	.	.	
Chrysomelidae	<i>Chrysolina fastuosa</i> (Scopoli, 1763)	2	
Chrysomelidae	<i>Chrysolina limbata</i> (Fabricius, 1775)	1	
Chrysomelidae	<i>Chrysolina pseudolurida</i> (Roubal, 1917)	1	
Chrysomelidae	<i>Chrysolina staphylaea</i> (Linnaeus, 1758)	1	2	
Chrysomelidae	<i>Galeruca pomonae</i> (Scopoli, 1763)	40	1	.	.	.	2	
Chrysomelidae	<i>Galeruca tanaetii</i> (Linnaeus, 1758)	.	.	1	.	.	2	
Chrysomelidae	<i>Longitarsus</i> sp.	1	
Coccinellidae	<i>Coccinella septempunctata</i> Linnaeus, 1758	1	.	.	
Coccinellidae	<i>Hippodamia variegata</i> (Goeze, 1777)	1	
Coccinellidae	<i>Symnus frontalis</i> (Fabricius, 1787)	2	.	.	5	.	.	1	.	.	.	
Cryptophagidae	<i>Cryptophagus</i> sp.	.	.	14	.	.	1	14	2	.	.	
Curculionidae	<i>Cycloderes pilosulus</i> (Herbst, 1796)	1	.	.	
Curculionidae	<i>Hypera postica</i> (Gyllenhal, 1813)	.	.	.	1	
Curculionidae	<i>Lixus</i> sp.	
Curculionidae	<i>Otiorhynchus conspersus</i> (Herbst, 1795)	1	.	.	.	
Curculionidae	<i>Otiorhynchus velutinus</i> Germar, 1824	.	.	3	.	.	.	1	.	.	.	
Curculionidae	<i>Sitona</i> sp.	1	.	.	
Curculionidae	<i>Trachyploceus alternans</i> Gyllenhal, 1834	10	3	.	9	.	2	.	4	.	.	
Dermestidae	<i>Dermestes lanarius</i> Illiger, 1801	5	3	2	14	1	5	1	3	.	.	
Endomychidae	<i>Lyoperdina succincta</i> (Linnaeus, 1767)	.	.	1	1	.	2	.	1	.	.	
Leiodidae	<i>Sciodrepoides watsoni</i> (Spence, 1813)	1	
Scarabaeidae	<i>Sisyphus schaefferi</i> (Linnaeus, 1758)	1	.	.	
Silphidae	<i>Nicrophorus antennatus</i> (Reitter, 1885)	.	.	3	.	.	2	
Silphidae	<i>Nicrophorus interruptus</i> Stephens, 1830	.	.	2	
Silphidae	<i>Nicrophorus investigator</i> Zetterstedt, 1824	4	2	.	.	.	3	
Silphidae	<i>Nicrophorus vestigator</i> Herschel, 1807	1	
Staphylinidae	<i>Staphylinidae</i> spp	1	4	1	22	11	8	7	12	18	.	
Tenebrionidae	<i>Blaps halophila</i> Fischer von Waldheim, 1820	.	.	2	
Tenebrionidae	<i>Blaps lethifera</i> Marsham, 1802	.	.	3	.	.	2	
Tenebrionidae	<i>Opatrum sabulosum</i> (Linnaeus, 1760)	1	.	1	1	2	1	1	1	1	1	
Tenebrionidae	<i>Pedinus femoralis</i> (Linnaeus, 1767)	6	.	.	2	1	
Trogidae	<i>Trox hispidus</i> (Pontoppidan, 1763)	4	1	1	.	1	1	
Total beetle taxa (species)		21 (19)	11 (10)	20 (17)	16 (14)	18 (16)	28 (24)	18 (14)	19 (14)	11 (10)		
Total individuals of beetles		110	55	133	134	84	155	110	133	85		

Family	Species	Study plot / Conditional control											
		SP13	SP14	SP15	SP16	SP18	CC14	CC15	CC16	CC18			
Alydidae	<i>Alydus calcaratus</i> (Linnaeus, 1758)	3	.	3	3	1
Anthrocoridae	<i>Orius niger</i> (Wolff, 1811)	2
Coreidae	<i>Bothrostethus annulipes</i> (Herrich-Schäffer, 1835)	1
Lygaeidae	<i>Emblethis griseus</i> (Wolff, 1802)	1	.	.	.
Lygaeidae	<i>Emblethis proximus</i> Seidenstücker, 1967	.	.	2	1	4	.	.	4
Lygaeidae	<i>Emblethis verbasci</i> (Fabricius, 1803)
Lygaeidae	<i>Ortholomus punctipennis</i> (Herrich-Schäffer, 1838)	.	.	4
Lygaeidae	<i>Pterotmetus staphyliniformis</i> (Schilling, 1829)	1	.	.	.
Lygaeidae	<i>Raglius alboacuminatus</i> (Goeze, 1778)	1
Lygaeidae	<i>Tropidophlebia costalis</i> (Herrich-Schäffer, 1850)	1
Lygaeidae	<i>Xanthochilus quadratus</i> (Fabricius, 1798)	.	1	2	.	.	17	1	1
Miridae	<i>Psallus</i> sp.	1	.
Nabidae	<i>Prostemma sanguineum</i> (Rossi, 1790)	.	.	.	1	.	1
Pentatomidae	<i>Sciocoris cursitans</i> (Fabricius, 1794)	1	1
Pentatomidae	<i>Zicrona caerulea</i> (Linnaeus, 1758)	.	.	1
Reduviidae	<i>Covanus contrarius</i> Reuter, 1881	1	1	.	.	.
Tingidae	<i>Lasiantha capucina</i> (Germar, 1837)	2
Auchenorrhyncha		36	7	103	17	4	37	6	12
Mutillidae	<i>Physetopoda balensis</i> (Fabricius, 1787)	1
Mutillidae	<i>Ronisia brutia</i> (Petagna, 1787)	1
Myrmeleontidae (larva)		.	.	.	1
Acridoidea		17	34	61	48	85	19	76	14	35	.	.	.
Gryllidae	<i>Gryllus campestris</i> Linnaeus, 1758	.	.	.	8	1	.	1	4
Gryllidae	<i>Melanogryllus desertus</i> (Pallas, 1771)	2
Oecanthidae	<i>Oecanthus pellucens</i> (Scopoli, 1763)	1
Tertigonioidae		.	.	2	1
Total insect taxa (species)		27 (23)	14(11)	27 (21)	24 (18)	24 (20)	35 (29)	26 (20)	27 (19)	14 (12)	.	.	.
Total individuals		170	97	310	215	177	233	199	171	125	.	.	.