



Differences in arthropod communities between grazed areas and grazing exclosures depend on arthropod groups and vegetation types

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ABSTRACT

Livestock grazing is one of the most common management practices for grasslands and can greatly affect their biodiversity. However, arthropod diversity response patterns to grazing regimes are difficult to predict. We conducted a short-term grazing exclusion experiment in traditionally managed alkali grasslands in Hungary to investigate differences between grazed and ungrazed vegetation for different arthropod groups. The experiment was laid out in a full factorial design, with twelve 50 × 100 m short-term grazing exclosures in vegetation types with high (alkali wet meadow) and low productivity (alkali steppe). We sampled ground beetles and spiders with pitfall traps and true hoppers by sweep netting. We used vegetation type (wet meadow vs dry steppe), management (grazed vs ungrazed) and their interaction as fixed effects in mixed models. We found higher species richness and activity density of spiders and ground beetles in the more productive wet meadow vegetation, where the community structure of each arthropod group also shifted toward hygrophilous species. Significant interactions between vegetation type and management indicated a dependence of management effects on vegetation types: arthropod community structure shifted towards hygrophilous species in ungrazed meadows, but not in ungrazed steppe sites. True hopper abundance was higher in grazed meadow sites, but lower in grazed steppe sites, compared to ungrazed sites. True hopper community structure shifted toward generalist herbivores in ungrazed sites, regardless of vegetation type. We concluded that vegetation types determine arthropod communities and modulate the effects of grazing on arthropods. Our results suggest that moderate disturbance from low-intensity grazing has a positive or neutral effect in wetter, more productive vegetation, but a negative or neutral effect in drier, less productive vegetation, depending on the arthropod group. Herbivorous insects that dwell on plants are particularly affected by management because they are more susceptible to direct impacts, such as unintentional predation by grazing cattle, and because of asymmetrical competition between mammalian and insect herbivores.

1. Introduction

Grasslands are important and widespread ecosystems worldwide, playing an important role in many ecosystem services and contributing greatly to biodiversity (Bengtsson et al., 2019; Zhao et al., 2020). Management, such as livestock grazing, is one of the most important drivers in grasslands and affects many ecosystem properties, including

soil, microclimate, biomass, and biodiversity (Dengler et al., 2014; McDonald et al., 2019; Valkó et al., 2018). Arthropods are essential components of grassland ecosystems and play a key role in ecosystem processes, health, and recovery. They are responsible for pollination, herbivory, decomposition, and nutrient cycling and are a food source for many vertebrates (Price et al., 2011; Yang and Gratton, 2014). However, the effects of grazing on species-rich invertebrate taxa, such as

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arthropods, are poorly understood, and the response patterns of their diversity to grazing regimes are hard to predict (van Klink et al., 2015; Wang and Tang, 2019). Livestock grazing can affect arthropod communities in several ways. Trampling of grazing animals and accidental ingestion of arthropod individuals act as direct mortality factors and can reduce arthropod populations. These impacts are more significant for species with limited mobility or immobile developmental stages, whereas most arthropods can escape by jumping, flying, or dropping off plants (Gish et al., 2010, 2011). Indirect effects operate through changes in vegetation characteristics and abiotic conditions and can be either beneficial or detrimental to arthropods. On the one hand, grazing can result in patchy vegetation, creating a more heterogeneous environment that supports more arthropod species (Jerrentrup et al., 2014; Wallis De Vries et al., 2007). On the other hand, grazing can cause a negative cascading effect along the entire food web by depleting plant biomass (Pringle et al., 2007; Vandegehuchte et al., 2017). Both direct and indirect effects increase with increasing grazing intensity (Iussig et al., 2015; van Klink et al., 2015). Therefore, grazing intensity and livestock species are key components in grazing systems (Boschi and Baur, 2007; Jerrentrup et al., 2015; van Klink et al., 2016; Menard et al., 2002; Öckinger et al., 2006; Rook et al., 2004). However, arthropod response to grazing or its abandonment may depend on the arthropod groups studied and the vegetation types they inhabit (Daskin and Pringle, 2016; Schmidt et al., 20122; Sjödin et al., 2008). It is well known that vegetation type characteristics, such as plant species richness and composition, vegetation structure and architecture, strongly influence arthropod communities (Ebeling et al., 2018; Rosas-Ramos et al., 2018; Torma et al., 2014). Interactions between grazing management and vegetation types can help understand grassland community responses to grazing. For example, Schmidt et al. (2012) found high ant abundance and diversity in grazed high-productivity vegetation, in contrast to low-productivity vegetation where grazing reduced their numbers. Short and tall grass vegetation types have different vegetation structures and can provide different abiotic conditions, food resources, and predation risks for arthropods, which are reflected in arthropod community composition and diversity (Ford et al., 2013; van Klink et al., 2013; Torma et al., 2017, 2019). Mosaics of short and tall vegetation types in semi-natural grasslands are often created by livestock grazing. A number of studies have investigated whether these vegetation mosaics created by grazing can promote arthropod diversity (Ford et al., 2013; van Klink et al., 2013; Sjödin et al., 2008; Wallis De Vries et al., 2016). However, different vegetation types in naturally heterogeneous grasslands may have evolved according to environmental gradients even without the intervention of livestock grazing. Grazing in these naturally evolved vegetation mosaics provides an exceptional opportunity to examine whether the effects of grazing management on arthropod communities depend on vegetation types.

The effects of low to moderate grazing disturbance on plant diversity tend to be positive in wet, tall grasslands and negative in dry, short, and less productive grasslands (Adler et al., 2005; Cingolani et al., 2005; Gao and Carmel, 2020; Lezama et al., 2014; Milchunas et al., 1988; Milchunas and Lauenroth, 1993; Olf and Ritchie, 1998). Presumably, arthropods also respond differently to grazing disturbance in high- and low-productivity vegetation. However, there are few studies that address arthropod response to different grazing interventions in high- and low-productivity vegetation types (but see Báldi et al., 2013). To our knowledge, the interactions between grazing management and vegetation productivity on the biodiversity of arthropods comprising more than one arthropod group have not yet been studied in field experiments. To fill this knowledge gap, we conducted a short-term grazing exclusion experiment in Pannonian alkali grasslands.

Pannonian alkali grasslands are among the priority habitats of Annex 1 of the European Union Habitats Directive (Pannonic salt steppes and salt marshes (1530 *)). They are also important resting sites for many migratory birds; therefore, they are particularly important for the Natura 2000 network. These traditionally used alkali pastures can

harbour numerous species that have disappeared elsewhere due to intensification and homogenisation of land use (Báldi et al., 2013). According to their diverse microtopography and the salt and water content of the soil, alkali habitats are characterised by a mosaic of vegetation patches with different compositions (Deák et al., 2014; Tóth, 2010). Wet alkali meadows and dry alkali shortgrass steppes (hereafter referred to as “salt meadow” and “salt steppe”, respectively) cover the majority of alkali habitats in Hungary. Salt meadow patches have developed in depressions, but at somewhat higher elevations than marshes. The water table is generally near the surface. Salt meadow vegetation dominated by the grass *Alopecurus pratensis* L. is typically tall and dense, producing high plant biomass (Kelemen et al., 2013). Salt steppes have developed at relatively high elevations of the microrelief and are characterised by sparse vegetation. The dominant grass species is the short-growing *Festuca pseudovina* Hack. ex Wiesb., and characteristic subordinate plants are *Artemisia sanctonicum* L. (*Artemisia* steppes) and *Achillea* spp. (*Achillea* steppes).

The mosaic of salt meadow and salt steppe vegetation patches made the Pannonian alkali grassland an ideal experimental study system, ensuring identical baseline conditions for high productivity (salt meadow) and low productivity (salt steppe) sampling sites in terms of surrounding landscape features and land use history. Landscape features are known to influence the effects of management on biodiversity (Batáry et al., 2007; Kőrösi et al., 2012; Söderström et al., 2001).

Arthropod response to grazing can be taxon-specific and depends on habitat preferences determined by species morphology, physiology, and ecological characteristics (Schoonhoven et al., 2005). Therefore, information on which species and taxonomic and functional groups are sensitive to or tolerate disturbance from grazing is essential. Indicator species provide valuable information for assessing “winners” and “losers” in environments altered by grazing and can serve as potential surrogates for future monitoring (Enkhtur et al., 2017). Multitaxa and trait-based approaches are essential for better understanding the effects of management on arthropods in general; they provide more reliable information than species richness patterns of individual taxonomic groups (van Klink et al., 2015). Species richness is an important and widely used measure of community response to disturbance. However, changes in abundance and community composition, and the resulting shifts in the distribution of morphological and ecological traits of species, are also important consequences of disturbance and may indicate it more sensitively (Chillo et al., 2017; Scohier and Dumont, 2012). To reveal differences in arthropod communities, we compared species richness, abundance, and community-weighted means (CWM) of arthropod trait values between grazed and ungrazed plots. We characterised species using three commonly accepted traits that generally reflect species adaptation to environmental conditions: body size, trophic behaviour, and moisture preference (Gallé and Batáry, 2019). We selected three arthropod groups for study: spiders (Araneae), ground beetles (Coleoptera: Carabidae), and true hoppers (Hemiptera: Auchenorrhyncha). They are species-rich and abundant in grasslands and play different roles in ecosystem functioning. Spiders and ground beetles are common predatory arthropods in many terrestrial ecosystems, although some ground beetle species are granivorous or omnivorous. Spiders and ground beetles are often used as indicators of environmental change because they are sensitive to changes in vegetation structure, microclimate, and biological environment (Buchholz, 2010; Kotze et al., 2011). True hoppers are particularly abundant and species-rich in grassland ecosystems, providing a rich prey source for many predators. They are important primary consumers and respond rapidly to vegetation changes caused by grassland management. For these reasons, they are increasingly used for biomonitoring and community ecology studies in grasslands (Bartlett et al., 2018; Biedermann et al., 2005).

We assumed differences in characteristic species and arthropod community structure between vegetation types. We predicted that in salt steppes (low-productivity vegetation), exclusion of livestock may increase species richness and abundance of arthropods, in contrast to salt

meadows (high-productivity vegetation), where low-intensity grazing may diversify arthropod communities. Using selected arthropod groups and species traits, we tested the following specific hypotheses: (1) differences in management, i.e. grazing vs exclusion from grazing, have a stronger effect on true hoppers, which mostly live in and directly feed on vegetation, compared to spiders and ground beetles, which are primarily predatory and active on the ground; (2) lack of disturbance from grazing results in a shift toward hygrophilous species in exclosures because grazing can create patches with drier microclimate; and (3) toward larger species because large species are generally more sensitive to disturbance.

2. Materials and methods

2.1. Study region and sites

The “Csanádi puszták” Protected Area is located in the southern part of the Great Hungarian Plain (Fig. 1). The region lies at 80–108 m a.s.l. and has a temperate continental climate with warm and dry summers with at least one month of drought and cold winters. The mean annual temperature is 10.3–10.5 °C, and the annual precipitation is 350–550 mm (Dövényi, 2010). In the region, the predominant natural open habitat type was steppe on loess soil, but alkali vegetation on solonetz soil also developed in deflations. Large parts of the loess steppe were converted into arable land, but in some places like Csanádi puszták the original vegetation of alkali grasslands has been preserved. Csanádi puszták, with a total area of 4057 ha, consists of three slightly separated grassland areas, namely Kopáncs, Montág and Királyhegyesi puszták (Fig. 1). Salt meadows and steppes occupy 22.1% and 26.5% of the protected area, respectively (Molnár et al., 2016). Salt ponds and marshes, loess steppes, and atypical dry and semi-dry grasslands also occur on smaller area in the protected zone. Our study was conducted in grassland areas (Királyhegyesi and Montág) where Hungarian Grey cattle, the traditional beef cattle of the Carpathian Basin, have been raised since 2006. Previously, mixed cattle and sheep farming was practised. However, the local robust cattle breeds were considered more suitable for grassland management (Kovácsné Koncz et al., 2014). The stocking density was less than 0.5 animals per hectare.

2.2. Experimental design

We conducted an experiment with a full factorial design. Before the start of the grazing season in spring 2018, we fenced six 50 × 100 m plots in each grassland area (Királyhegyesi and Montág) with a

minimum distance of 100 m between each other, resulting in a total of 12 livestock exclosures. In each grassland area, three exclosures were established in the salt steppe and three exclosures in the salt meadow vegetation. We considered one exclosure and the adjacent grazed area as one sampling site (N = 12). In Királyhegyesi puszták, the grazing season started later due to a decision of the National Park Administration. After one month of grazing, arthropod samples were collected at four locations of each sampling site, i.e. in both the fenced and grazed parts of the sites closer to the fence and farther away. In order to use two different collection methods for arthropods without interfering with each other, we divided the sampling sites into two equal parts for the collection methods (Fig. 1).

Spiders and ground beetles were sampled using pitfall traps (white 500 ml plastic cups, 8.5 cm in diameter) filled with a 50% ethylene glycol–water solution containing a few drops of an odourless detergent. The traps were equipped with transparent plastic funnels to reduce vertebrate bycatch, and a plastic roof was placed over each trap to prevent dilution of the preservative (Császár et al., 2018). In each location within the sites, four traps were placed in a row 10 m apart, resulting in a total of 192 traps. The traps were active for 13 days. Traps were set from 10 to 23 May and from 8 to 21 June in the Királyhegyesi puszták and the Montág puszták, respectively. True hoppers were collected with sweep nets with a diameter of 40 cm. Sweeping is a widely used method for sampling plant-dwelling arthropods, including hemipterans (Stewart, 2002). In each location within the sites, 75 sweeps were performed between 10 am and 4 pm on sunny, windless days (10 May and 9 June 2018). Collected material was placed in plastic bags filled with 70% ethanol and identified to species level by the experts (see Table A1).

2.3. Arthropod traits

We characterised species by body size, moisture preference, and trophic behaviour. For body size, we used the mean body length of the species in mm. We classified species into three or five categories (xerophilous to hygrophilous) based on their moisture preference. We defined feeding behaviour of taxa differently. We divided ground beetle species into categories corresponding to trophic guilds, i.e. as herbivores, omnivores, and carnivores. We distinguished between web-building and actively hunting spiders based on their hunting strategy. Based on their host plant range, we classified true hopper species into monophagous, oligophagous, and polyphagous categories. Detailed information on arthropod trait categories and literature sources can be found in the supplementary material (Table A1).

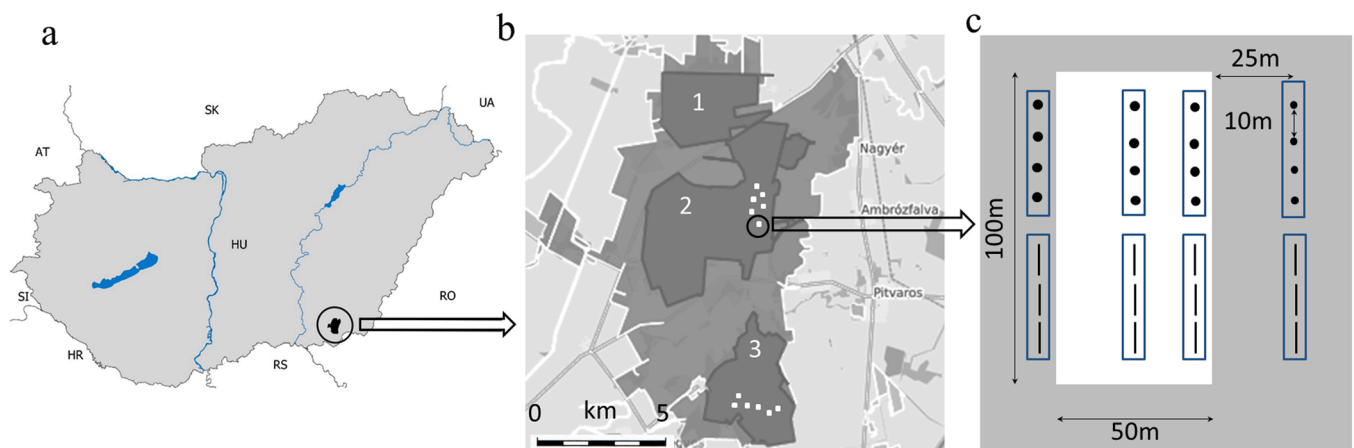


Fig. 1. (a) – A map showing the location of the “Csanádi puszták” Protected Area in Hungary. (b) – A map of the “Csanádi puszták” Protected Area showing the grassland areas, namely Kopáncs (1), Montág (2) and Királyhegyesi (3). White dots mark fenced grazing exclosures. (c) – A schematic figure of sampling design. The white area represents an established grazing exclosure, black dots and lines represent pitfall traps and sweeping transects, respectively. The framed pitfall traps and sweeping transects represent sample units.

2.4. Data analyses

Arthropod species data were pooled by sampling locations, resulting in 4×12 statistical samples for statistical analyses (Fig. 1). We used the community-weighted mean approach (CWM) to examine trait-environment relationships. CWM summarises shifts in mean trait values within communities due to environmental selection for certain traits, and this method is commonly used in community-level studies (Ricotta and Moretti, 2011). We calculated CWM trait values using the R package FD (Laliberté et al., 2014). To identify species associated with grazed and ungrazed meadow and steppe vegetation, we used the indicator species approach of Dufrêne and Legendre (1997). In this method, indicator values are calculated by combining the abundance of the species in a given site group (specificity) and the probability of finding the species at sites belonging to that site group (fidelity). We used the *multipatt* function in the R package indicispecies (De Cáceres and Legendre, 2009). The function searches for indicator species for both individual site groups and combinations of site groups (De Cáceres et al., 2010). To analyse differences in arthropod communities, we used linear mixed models (LMMs) and generalised linear mixed models (GLMMs) in

the R package lme4 (Bates et al., 2015). In the case of count data, we used Poisson models, and in the case of data overdispersion, we used negative binomial models with *glmer* and *glmer.nb* functions, respectively. We used species richness, abundance (activity-density in the case of spiders and ground beetles), and CWM trait values of arthropod groups as response variables, and vegetation type (meadow vs steppe), management (grazed vs ungrazed), and their interaction as fixed effects. Possible spatial autocorrelation between sites was accounted for by adding experimental sites nested in grasslands as a random effect. In the case of significant interaction terms, we performed post-hoc comparisons (Kenward-Roger method) to separately detect differences between grazed and ungrazed sites in the different vegetation types. For this purpose, we used the *emmeans* function in the R package emmeans (Lenth, 2020). We performed all analyses in R version 4.0.2. (R Core Team, 2020).

Table 1

Association between arthropod species and groups of grazed salt steppe, ungrazed salt steppe, grazed salt meadow, and ungrazed salt meadow according to the extended Indicator Value method. Only significant associations are shown. Abbreviations: stat – indicator value of species; A, B – two components of the indicator value, ‘specificity’ and ‘fidelity’, respectively.

Taxa	steppe		meadow		P	stat	A	B
	grazed	ungrazed	grazed	ungrazed				
CARABIDAE								
<i>Agonum viridicupreum</i>			+	+	0.0022	0.736	1	0.542
<i>Amara chaudiroi</i>			+	+	0.0002	0.970	0.982	0.958
<i>Brachinus psophia</i>			+	+	0.0002	0.864	0.995	0.75
<i>Brachinus elegans</i>			+	+	0.0006	0.861	0.988	0.75
<i>Chlaenius nigricornis</i>			+	+	0.0646	0.528	0.957	0.292
<i>Diachromus germanus</i>			+	+	0.0004	0.836	0.987	0.708
<i>Harpalus cupreus</i>			+	+	0.0002	0.883	0.986	0.792
<i>Harpalus flavicornis</i>	+	+	+		0.0002	0.966	0.959	0.972
<i>Harpalus pygmaeus</i>	+	+			0.0002	0.883	0.984	0.792
<i>Harpalus rubripes</i>	+	+			0.0238	0.662	0.878	0.5
<i>Harpalus subcylindricus</i>	+	+	+		0.0128	0.777	0.989	0.611
<i>Microlestes minutulus</i>			+		0.0038	0.683	0.7	0.667
<i>Poecilus cupreus</i>			+	+	0.0002	0.816	1	0.667
<i>Pterostichus anthracinus</i>			+	+	0.0200	0.577	1	0.333
<i>Pterostichus chameleon</i>			+	+	0.0102	0.612	1	0.375
<i>Syntomus obscuroguttatus</i>			+	+	0.0328	0.579	0.895	0.375
ARANEAE								
<i>Argenna patula</i>			+	+	0.0170	0.577	1	0.333
<i>Clubiona diversa</i>		+			0.0096	0.589	0.833	0.417
<i>Diplostyla concolor</i>				+	0.0020	0.697	0.971	0.5
<i>Drassyllus lutetianus</i>			+	+	0.0148	0.577	1	0.333
<i>Drassyllus sur</i>	+	+			0.0132	0.726	0.792	0.667
<i>Euophrys frontalis</i>	+	+			0.0074	0.636	0.971	0.417
<i>Euryopis quinqueguttata</i>	+	+			0.0032	0.645	1	0.417
<i>Micaria pulicaria</i>				+	0.0306	0.509	0.778	0.333
<i>Oedothorax apicatus</i>			+	+	0.0660	0.557	0.932	0.333
<i>Ozyptila trux</i>			+	+	0.0002	0.837	0.99	0.708
<i>Pachygnatha degeeri</i>			+	+	0.0002	0.901	0.974	0.833
<i>Pardosa agrestis</i>			+	+	0.0002	0.952	0.946	0.958
<i>Pardosa prativaga</i>			+	+	0.0022	0.677	1	0.458
<i>Silometopus curtus</i>			+	+	0.0208	0.577	1	0.333
<i>Trochosa ruficola</i>			+	+	0.0170	0.688	0.947	0.5
<i>Zelotes mundus</i>			+	+	0.0004	0.731	0.987	0.542
AUCHENORRHYNCHA								
<i>Artianus interstitialis</i>	+	+	+		0.0006	0.885	0.973	0.806
<i>Chlorita prasina</i>	+	+			0.0024	0.784	0.867	0.708
<i>Cicadula placida</i>			+	+	0.0090	0.612	1	0.375
<i>Doratura homophyla</i>	+	+	+		0.0002	0.976	0.952	1
<i>Graphocraerus ventralis</i>	+	+	+		0.0280	0.782	0.958	0.639
<i>Hephathus nanus</i>	+	+			0.0722	0.532	0.97	0.292
<i>Kelisia praecox</i>			+	+	0.0188	0.577	1	0.333
<i>Laburru handlirshi</i>	+	+			0.0006	0.912	0.907	0.917
<i>Mendraus paucillus</i>	+	+			0.0082	0.642	0.988	0.417
<i>Psammotettix kolosvarensis</i>			+	+	0.0014	0.727	0.976	0.542
<i>Rhopalopyx vitripennis</i>	+	+			0.0280	0.796	0.761	0.833

3. Results

3.1. Ground beetles

We collected 4241 individuals belonging to 59 ground beetle species (Table A2). In the salt meadow vegetation, the most frequent species were *Brachinus elegans* Chaudoir, 1842, *Agonum viridicupreum* (Goeze, 1777), and *B. psophia* Audinet-Serville, 1821, with a frequency of 21.1%, 15.4%, and 13.2%, respectively. In the salt steppe vegetation, *Harpalus subcylindricus* Dejean, 1829 (4.8%), *B. crepitans* (Linnaeus, 1758) (4.4%), and *H. flavicornis* Dejean, 1829 (3.2%) were the most frequent species. According to the IndVal analyses, we found other species associated with meadow or steppe vegetation (Table 1). In general, ground beetles associated with meadow vegetation were meso- and hygrophilous, mostly predatory species. In contrast, species associated with steppe vegetation were xero- and subxerophilous omnivores and seed predators. Of the species associated with steppe, *H. subcylindricus* and *H. flavicornis* were also associated with grazed meadow vegetation.

We captured more species and specimens in salt meadow vegetation than in salt steppe vegetation (Table 2, Fig. 2). We found that the community structure of ground beetles in the steppe vegetation was shifted towards xerophilous species compared to the meadow vegetation. In addition, a significant difference in CWM moisture preference of ground beetles was found between grazed and fenced areas, indicating the effects of the grazing exclusion. However, this effect was modulated by vegetation type: the community structure of ground beetles was shifted towards hygrophilous species in ungrazed meadow vegetation, but not in ungrazed steppe vegetation, as revealed by post-hoc comparisons (Fig. 2c). In the other cases, we did not detect any significant effects (Table 2).

3.2. Spiders

We collected 4874 adult individuals of 80 spider species (Table A2). The most frequent species were *Aulonia albigana* (Walckenaer, 1805) (30.0%), *Trochosa robusta* (Simons, 1876) (16.3%), and *Metopobactrus deserticola* Loksa, 1981 (9.0%) in both vegetation types. However, several less frequent species were associated with the salt meadow or salt steppe vegetation, and some of them were significantly associated with the ungrazed vegetation (Table 1). Most of the spiders associated

with salt meadow vegetation preferred moist or semihumid habitats. However, we also found several generalist species (e.g. *Oedothorax apicatus* (Blackwall, 1850), *Pachygnatha degeeri* Sundevall, 1830) and species with preferences for dry habitats (e.g. *Silometopus curtus* (Simons, 1881), *Zelotes mundus* (Kulczyński, 1897)) among the indicator species in the meadow vegetation.

We found that species richness and activity density of spiders were significantly higher in meadow vegetation, and according to the values of CWM, hygrophilous spiders were more frequent there (Table 2, Fig. 2). Similar to ground beetles, the CWM moisture preference of spiders was significantly affected by management and its interaction with vegetation type. The community structure of spiders shifted towards hygrophilous species in ungrazed meadow vegetation, but not in ungrazed steppe vegetation (Fig. 2c). No significant effects were detected in the other cases (Table 2).

3.3. True hoppers

We collected 4603 individuals of 54 species (Table A2). The most abundant species, *Laburris handlirschi* (Matsumura, 1908) (26.3%), a xerophilous species feeding exclusively on *Artemisia* spp., was associated with salt steppes (Table 1). Other abundant species, e.g. the mesophilous, polyphagous *Reptalus quinquecostatus* (Dufour, 1833) (19.1%), and the xerophilous, oligophagous grass-feeder, *Doratura homophyla* (Flor, 1861) (10.0%) were common in both vegetation types. However, *D. homophyla* was associated only with the grazed parts of the meadow vegetation. Two other oligophagous grass-feeding species associated with steppe vegetation, whether grazed or not, were also associated with the grazed meadow vegetation. Several other species indicated either salt steppe or meadow vegetation regardless of grazing (Table 1). Steppe-associated species were xerophilous, and many were exclusively associated with *Festuca* (e.g. *Mendraus pauxillus* (Fieber, 1869), *Rhopalopyx vitripennis* (Flor, 1861)), or *Artemisia* (e.g. *L. handlirschi*, *Chlorita prasina* Fieber, 1884, *Hephathus nanus* (Herrich-Schäffer, 1835)) as host plants. Indicator species in meadow vegetation were meso- and hygrophilous species feeding on many monocotyledonous plants (Poaceae, Cyperaceae); only *Kelisia praecox* Haupt, 1935 is known to feed exclusively on sedges (*Carex* spp.).

We found significant differences in total abundance, CWM moisture preference, and CWM trophic niche width of true hoppers between

Table 2

Effects of vegetation type (salt meadow vs salt steppe), management (grazed vs ungrazed) and their interaction on different arthropod groups according to LMMs and GLMMs. Significant results are marked in bold.

	vegetation type (salt meadow vs. salt steppe)			management (grazed vs. ungrazed)			vegetation type × management		
	est. (± SE)	t or z	P	est. (± SE)	t or z	P	est. (± SE)	t or z	P
CARABIDAE									
species richness ^p	-0.654 (0.148)	4.404	< 0.001	-0.024 (0.110)	0.221	0.825	0.182 (0.181)	0.999	0.318
activity-density ^{nb}	-1.240 (0.480)	2.583	0.010	0.2137 (0.245)	0.870	0.385	-0.1453 (0.354)	0.410	0.682
size	-0.857 (0.501)	1.713	0.099	-0.258 (0.458)	0.563	0.577	0.708 (0.647)	1.093	0.282
moisture preference	-0.620 (0.081)	7.584	< 0.001	-0.163 (0.054)	2.961	0.006	0.161 (0.077)	2.061	0.047
feeding behaviour	-0.068 (0.063)	1.088	0.292	0.001 (0.045)	0.022	0.983	-0.030 (0.064)	0.464	0.646
ARANEAE									
species richness ^p	-0.284 (0.097)	2.899	0.004	-0.064 (0.092)	0.691	0.489	0.008 (0.140)	0.054	0.957
activity-density ^{nb}	-0.414 (0.163)	2.521	0.012	-0.135 (0.162)	0.831	0.406	0.081 (0.231)	0.347	0.728
size	-0.406 (0.369)	1.100	0.281	0.194 (0.361)	0.538	0.594	0.537 (0.511)	1.051	0.301
moisture preference	-0.275 (0.062)	4.422	< 0.001	-0.171 (0.037)	4.503	< 0.001	0.163 (0.053)	3.050	0.004
feeding behaviour	-0.007 (0.067)	0.100	0.922	0.060 (0.050)	1.208	0.235	-0.013 (0.071)	0.183	0.856
AUCHENORRHYNCHA									
species richness ^p	0.123 (0.153)	0.800	0.424	0.122 (0.123)	0.991	0.322	-0.128 (0.173)	0.749	0.454
abundance ^{nb}	0.951 (0.422)	2.254	0.024	0.645 (0.162)	3.983	< 0.001	-0.969 (0.222)	4.364	< 0.001
size	-0.056 (0.214)	0.256	0.805	0.108 (0.167)	0.645	0.523	-0.149 (0.236)	0.630	0.533
moisture preference	-0.210 (0.048)	4.337	< 0.001	-0.139 (0.029)	4.728	< 0.001	0.102 (0.041)	2.436	0.020
feeding behaviour	-0.189 (0.063)	3.001	0.009	-0.113 (0.041)	2.717	0.010	0.091 (0.059)	1.545	0.131

^p – Poisson, ^{nb} – negative binomial distribution

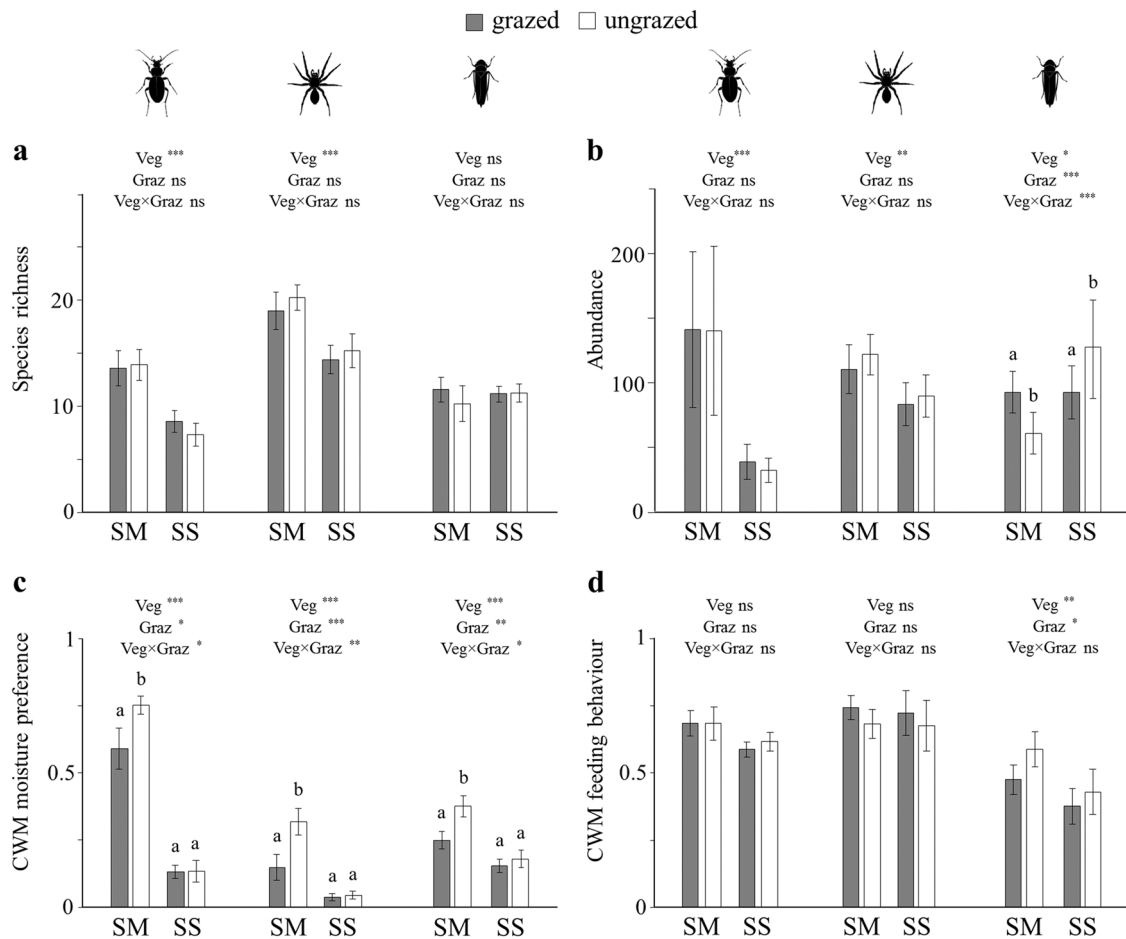


Fig. 2. Bar charts (mean ± SEM) showing differences in species richness (a), abundance (b), community-weighted mean values for moisture preference (c) and feeding behaviour (d) of arthropods sampled (ground beetles, spiders, and true hoppers). Significant effects of vegetation type (salt meadow vs salt steppe), grazing management (grazed vs ungrazed), and their interaction on arthropod groups are marked with asterisks (* < 0.05, ** < 0.01, *** < 0.001, ns – non-significant), based on the models in Table 1. Letters above bar charts indicate significant differences (P < 0.05) according to post-hoc comparisons implemented when significant interaction of grazing management and vegetation type was found (for more detailed information see the Table A3). Abbreviations: SM – salt meadow, SS – salt steppe, Veg – vegetation type, Graz – grazing management.

meadow and steppe vegetation (Table 2, Fig. 2). True hopper community was composed of more xerophilous species and more specialised herbivorous species in terms of host plant range in the steppe vegetation compared to the meadow vegetation. Management had a significant effect on the abundance of true hoppers. Their abundance was lower in grazed steppe than in ungrazed steppe vegetation, but higher in grazed than in ungrazed meadow vegetation, due to the interaction of management and vegetation type (Fig. 2b). Significant differences between grazed and ungrazed vegetation were found in CWM moisture preference and CWM trophic niche width of true hoppers (Fig. 2c,d). In ungrazed vegetation, community structure shifted towards less specialised herbivorous species, regardless of vegetation type. However, the significant interacting effect of management and vegetation type on moisture preference CWM showed that the true hopper community was composed of more hygrophilous species in the ungrazed meadow, but not in the ungrazed steppe vegetation (Fig. 2c). In other cases, no significant effects were detected (Table 2).

4. Discussion

We found significant interactions between the effects of vegetation type (salt meadow vs salt steppe) and management (grazed vs ungrazed) on arthropods. Management affected the community structure of all arthropod taxa studied only in the more productive salt meadow vegetation. In addition, short-term grazing exclusion negatively affected the

abundance of true hoppers in the salt meadow vegetation, while it had a positive effect in the less productive salt steppe vegetation, compared to grazing. These results suggest that arthropod community responses to management depend on vegetation productivity, although different arthropod groups responded differently to the presence or absence of grazing disturbance.

4.1. Vegetation types determine arthropod communities

The positive role of plant species diversity and green plant biomass for herbivorous insects is well known (Lawton, 1983; Root, 1973; Siemann et al., 1998), while structural complexity of vegetation is particularly important for carnivorous arthropods (Dennis et al., 1997). We found higher species richness and activity density of spiders and ground beetles in the tall meadow vegetation than in the sparse salt steppe vegetation. In addition to differences in vegetation characteristics, differences in soil and microclimatic conditions could also play an important role in the formation of spider and ground beetle communities (Pétillon et al., 2008; Torma et al., 2019). It is likely that species moisture preference is responsible for differences in ground beetle and spider communities between salt meadow and salt steppe vegetation. For example, soil moisture is critical for ground beetles because eggs absorb water from the environment to complete embryonic development, and larvae are sensitive to desiccation (Kotze et al., 2011). Moisture conditions are also critical for spiders (Entling, 2007).

In contrast to ground beetles and spiders, the abundance of true hoppers was higher in salt steppe vegetation. Presumably, narrower trophic specialisation of herbivorous species in salt steppes may offset the benefits of higher plant biomass in salt meadows in terms of herbivore diversity (Torma et al., 2017). The majority of true hopper species were generalist grass-feeders. However, especially in the steppe vegetation, we collected several species that were exclusively associated with fine-leaved *Festuca* and *Asteraceae* or *Artemisia*. Accordingly, we found more specialised herbivorous true hoppers in steppe than in meadow vegetation.

4.2. The effects of management on arthropods depend on vegetation types

We found differences in abundance patterns and related changes in trait composition of arthropod communities between grazed and ungrazed sites, but not in their species richness. A recent meta-analysis (Wang and Tang, 2019) found that grazing intensity primarily affects arthropod abundance. In addition, changes in species abundance can result in altered community structure and composition depending on species sensibility to grazing disturbance, even without changes in community species richness (Hemm and Höffer, 2012; Lyons et al., 2017).

We highlight that the significant effects of management on arthropods were dependent on vegetation types, except in the case of trophic specialisation of true hoppers. Regardless of vegetation types, we found a higher proportion of more specialised true hoppers in grazed vegetation. This is in agreement with the results of Nickel and Hildebrandt (2003), who also found the highest proportion of specialists among true hoppers in low-intensity pastures, compared to fallow or high-intensity grassland, and Körösi et al. (2012), who indicated that mainly specialised true hoppers benefited from extensive grazing in Hungarian pastures. In general, specialised insect herbivores follow species richness patterns of plants more closely, whereas generalists are more dependent on plant biomass production (Huston, 1979; Huston and Gilbert, 1996). Presumably, low-intensity grazing supports specialised insects by enhancing the species richness of their host plants, whereas increasing total plant biomass resulting from short-term grassland abandonment tends to benefit generalists (Pöyry et al., 2006). However, the mechanisms underlying the response patterns of generalists and specialised insects to grazing and abandonment may differ. Some plants produce secondary metabolites that are unattractive to grazing mammals, but usually also to generalist insect herbivores (Nykänen and Koricheva, 2004; Vicari and Bazely, 1993). However, specialised insect herbivores can tolerate or even benefit from these secondary compounds because of their adaptation to their host plants (Poelman et al., 2009). The significance of this explanation may be limited to insect herbivores that feed on dicotyledonous plants, as grasses are less effective at producing such compounds (Tschamtké and Greiler, 1995). However, the main species of arthropod communities in grasslands are generally common grass-feeders (Šeat et al., 2021; Torma and Császár, 2013; Tschamtké and Greiler, 1995). In addition, insects that suck xylem or phloem fluid, such as true hoppers, are less susceptible to secondary metabolites generally contained in leaf vacuoles than insects that consume all leaf tissue with their chewing mouthparts (Douglas, 2006; Verhoeven et al., 2009).

Competition for plant resources between herbivorous mammals and insects is asymmetrical (Gómez and González-Megías, 2002), which can easily lead to decreasing abundance of herbivorous insects (Ford et al., 2013; Huntzinger et al., 2008; Vandegehuchte et al., 2017). However, competitive relationships may depend on both mammalian and insect herbivore parties. Just as specialised and generalist insect herbivores exhibit different foraging strategies, mammalian species also differ in grazing behaviour or strategy. Cattle (bovines) are less selective grazers, so-called “mass-feeders”, that consume plants in proportion to their abundance (Dumont et al., 2011). Cattle grazing likely affects insects that are more concerned with total plant biomass, i.e. generalists. In

addition, asymmetrical competition has little significance for specialised insects that feed on plants less palatable to grazing mammals. Some specialists may even benefit from grazing if it reduces the abundance of competitors to their host plants (Nickel and Hildebrandt, 2003; Pöyry et al., 2006). The observed difference in true hopper community structure between the grazed sites and exclosures in our experiment was mainly caused by common, oligophagous grass-feeder and polyphagous species (e.g. *A. interstitialis*, *D. homophyla*), whereas the majority of common specialists, especially those feeding on *Artemisia*, a less palatable plant for cattle, were less affected by management (e.g. *L. handlirschi*, *Ch. prasina*, *H. nanus*). This finding suggests that asymmetrical competition may directly affect herbivorous insect communities, although some species are likely responding to altered vegetation structure and microclimate, and not necessarily to reduced nutrition.

4.3. Management effects in salt steppe

In dry steppe vegetation, only the abundance of true hoppers was higher in exclosures than in grazed sites. Spiders and ground beetles did not benefit from the lack of grazing disturbance, suggesting that low-intensity grazing may have no direct or indirect effects on them. The importance of direct grazing effects (i.e. trampling and unintentional predation) is highly dependent on arthropod species traits which determine the likelihood of encounters between arthropods and mammalian herbivores (Gómez and González-Megías, 2007). Despite sparse vegetation, ground-dwelling arthropods can easily hide, e.g., in soil crevices that characterise the soil surface in dry salt habitats, and a high proportion of the species collected are nocturnal, and their encounter with grazing animals are limited. Therefore, ground-dwelling spiders and ground beetles are less likely than plant-dwelling true hoppers to be affected by the adverse effects of accidental predation and trampling. However, pitfall traps do not adequately capture a number of web-building spiders, particularly orb-weaving spiders. These species are likely more sensitive to grazing because they are exposed to more direct grazing impacts, and grazing can reduce the availability of anchor points for web building by reducing the structural complexity of the vegetation.

In addition to the absence of trampling and unintentional predation, true hoppers may also benefit from the greater plant biomass in ungrazed vegetation. Reduced plant biomass due to grazing can directly reduce the population size of herbivorous insects (Gómez and González-Megías, 2002). Unlike sap-sucking herbivores, herbivorous ground beetles, as seed-eaters, are generally not directly affected by the amount of green plant biomass (Gómez and González-Megías, 2007).

Surprisingly, our results suggest that indirect effects of grazing, acting through changes in vegetation characteristics and abiotic conditions, are of limited importance to arthropod communities in salt steppe vegetation. Arthropod species are presumably well-adapted to the sparse vegetation with its dry and warm conditions, and the changes induced by low-intensity grazing in this harsh environment are not likely to be pronounced enough to cause differences in arthropod communities between grazed and ungrazed sites. It is suggested that in harsh environments, environmental constraints may be more important than disturbance from management in structuring arthropod communities (Pétillon et al., 2007; Torma et al., 2019).

4.4. Management effects in salt meadow

Species richness and abundance of spiders and ground beetles did not differ between grazed and ungrazed meadow vegetation, similar to steppe vegetation. However, the abundance of true hoppers was higher in the grazed meadow than in the ungrazed meadow vegetation, whereas the opposite pattern was observed in the steppe vegetation. Indirect effects (i.e. reduction in vegetation height due to grazing and associated microclimatic changes) had a greater impact on arthropod community structure in meadow vegetation than in steppe vegetation. It

is likely that the microclimatic conditions altered by grazing are more crucial in comparatively wetter habitats. On the one hand, reduced vegetation due to grazing may result in a warmer and drier microclimate (Yates et al., 2000; Vaieretti et al., 2018), leading to a lower proportion of arthropods that prefer moisture. On the other hand, lower vegetation is not detrimental to all arthropods. For example, visual hunter arthropods may benefit from reduced vegetation (Morris, 2000), and it may also be beneficial for species that prefer warmer and drier microclimates (Zhu et al., 2020). In the present study, some steppe-associated species were also able to colonise and use the grazed meadow vegetation in large numbers. This probably resulted in higher abundance of true hoppers in grazed meadow than in ungrazed meadow vegetation. In addition, plant biomass reduced by grazing is thought to recover quickly in highly productive vegetation due to nutrient-rich plant regrowth, which may positively affect herbivorous insects (Chase et al., 2000; Daskin and Pringle, 2016).

4.5. Limitations in generalisation of management effects on arthropods

Most studies have focused on conservation effects of grazing on arthropod communities to maximise their species diversity in the long term (Littlewood et al., 2012). Long-term effects of grazing are usually associated with changes in plant community composition and are considered to strongly influence arthropod communities (van Klink et al., 2015). Grazing mammals can directly reduce the population size of arthropod species (Gish et al., 2017), and/or induce movement of arthropod individuals, e.g. between grazed and ungrazed patches, to conditions most favourable for them (Zhu et al., 2020). Moreover, some adaptations in certain plant-dwelling insects to avoid or reduce the risk of inadvertent ingestion by mammalian herbivores are associated with high costs to individuals, suggesting that direct effects may be more important than assumed (Gish et al., 2010, 2011). Whether or not the importance of direct effects is underestimated, revealing immediate responses of arthropods to grazing management can help understand the underlying mechanisms that can lead to changes in arthropod communities, even over time (Gish et al., 2017; van Noordwijk et al., 2012). For example, Berman et al. (2018) showed that the immediate facilitative effect of cattle grazing on spring webworm caterpillars later determined the caterpillar population distribution over years.

The results of our short-term experiment cannot be extrapolated unreservedly to a longer time period, although they provide important information about which arthropod groups and underlying species traits are sensitive to grazing management and which tolerate grazing disturbance or benefit from grazing exclusion. However, other traits, such as phenology, overwintering strategy (Körösi et al., 2012; Littlewood, 2008), and dispersal ability (Cole et al., 2006; Novotný, 1994), may also play a role in arthropod responses. In addition, grazing mammals may provide special resources for certain arthropods and, in this way, influence arthropod communities. For example, the faeces of grazing mammals may provide resources for dung-dwelling insects; however, these potential benefits are precarious in modern livestock systems. Faeces from domesticated animals may contain residues of commonly used parasiticides, such as ivermectins, which can negatively impact dung inhabiting insects (Ambrozova et al., 2021; Verdú et al., 2018, 2020). These insects require special attention due to their paradoxical situation.

We emphasise that grazing impacts on arthropods are highly dependent on vegetation characteristics such as productivity (Bassett and Fraser, 2015; Schmidt et al., 2012), plant species richness and vegetation structure (Liu et al., 2015; Zhu et al., 2015). However, disentangling these effects on arthropods is difficult because of the close relationships among them (Fadda et al., 2008). Moreover, the relationship between them may not be linear, e.g. a humped-back relationship between productivity and species richness of vegetation types as in lowland grasslands of Hungary (Kelemen et al., 2013).

4.6. Management implications

We agree with the conclusion of previous studies on arthropods that management regimes under current conditions can maintain arthropod biodiversity in an extensive area of Pannonian salt grasslands (Batáry et al., 2007, 2008; Körösi et al., 2012; Torma et al., 2019). However, this does not exclude possible changes in the future. For example, climate change scenarios predict drought for the region, and weather extremes will occur more frequently in the future. Our results suggest that grazing has a greater impact on arthropod communities in wetter vegetation. Further studies, especially those focusing on the potential interactions between management and climatic conditions on grassland biodiversity, would be essential to assess whether current management regimes, including traditional ones, will help maintain biodiversity in the changing future (Csákvári et al., 2021).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2022.108222](https://doi.org/10.1016/j.agee.2022.108222).

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