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Species and functional diversity of arthropod assemblages (Araneae, Carabidae, Heteroptera and Orthoptera) in grazed and mown salt grasslands

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ABSTRACT

Grazing and mowing are widely applied management practices in semi-natural grasslands, which are one of the most important habitats for biodiversity conservation in Europe. Due to the decline in extensively grazing livestock numbers, an increasing area of formerly grazed grasslands has being used as mown grasslands. However, we have scarce information on how arthropod assemblages are influenced by mowing in formerly grazed pastures. We assessed the effects of mowing compared to grazing on the species richness, abundance and functional diversity of arthropods in three grassland complexes in Hungary. Since 2005, these salt grasslands have been divided into two management units: extensive grazing management has been continued in one part, while annual late cutting has been established in the other part. In each management unit five sites were sampled. Spiders and ground beetles were sampled using pitfall traps, orthopterans and true bugs were sampled using sweep nets twice before cutting in 2015. In total, the data relating to 12,576 adult individuals of 334 species were analysed using mixed-models. Plant-dwelling true bugs and orthopterans responded more sensitively to mowing than ground-dwelling spiders and ground beetles. Beside the general negative effect of mowing on the species richness and abundance of plant-dwelling arthropods, the shifts in the community weighted mean values of these assemblages suggested the importance of the body size, trophic behaviour and dispersal ability of species in the functional response of these assemblages to the different management regimes. Ground beetles and spiders were rather influenced by the differences in the moisture conditions and vegetation properties. Presumably, strong abiotic stressors such as drought can partly override management effects on ground-dwelling arthropods. The effect of uniform and simultaneous biomass removal on large areas, and the direct mortality caused by mowing was the most disadvantageous for plant-dwelling arthropods. Based on our results, traditional management practices should be prioritized in grassland conservation, as alternative management practices might be less effective in preserving grassland biodiversity.

1. Introduction

Recent studies from terrestrial habitats report a serious decline in the diversity of various arthropod groups (e.g. Goulson et al., 2008; Van Dyck et al., 2009), as well as in their overall biomass (Hallmann et al., 2017). Arthropods have a prominent role in the maintenance of a variety of ecosystem functions such as pollination, herbivory, detrivory and nutrient cycling (e.g. Yang and Gratton, 2014). Therefore, preserving their diversity and abundance should constitute a prime conservation priority.

Semi-natural grasslands, created and maintained by traditional land use practices, contribute highly to the conservation of the biodiversity of terrestrial arthropods in Europe (Littlewood et al., 2012). However, over the last few centuries the area and the naturalness of semi-natural grasslands has decreased across the whole of Europe, due to their transformation into arable fields and the intensification or cessation of

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management in the remaining areas (Báldi et al., 2013). Agri-Environmental Schemes (AES) of the European Union aim to reduce the negative impacts of agricultural activities on the native biota. These programs support the management of semi-natural grasslands, with the explicit intention of maintaining high biodiversity; a general principle behind these programs is the extensification of farming systems (Ekroos et al., 2014). Therefore, the majority of studies have focused on how certain management practices can be fine-tuned to promote arthropod biodiversity by varying management intensity, frequency, duration or seasonality (Littlewood at al., 2012; Tälle et al., 2018). Another relevant, albeit less frequently addressed aspect is the difference between the effects of different management practices, such as grazing and mowing, on biodiversity (Tälle et al., 2016). Comparing the effects of grazing and mowing on arthropod biodiversity is increasing in importance given that, as a result of the decline in grazing livestock numbers, mowing is currently practiced in an increasing area of formerly grazed grasslands as an alternative management practice (Morris, 2000).

In the European Union, inland salt grasslands, typical of the Pannonian biogeographical region, have a high conservational importance, and are thus listed among the priority habitats of Annex 1 of the Habitats Directive (Pannonic salt steppes and salt marshes (1530*); Council of European Communities, 1992). Given their diverse micro-topography, which has a significant effect on the vegetation through changes in soil salt content and moisture regimes, these grasslands are characterized by a complex mosaic of compositionally distinct vegetation patches (Deák et al., 2014a). Pannonic salt grasslands are traditionally used as extensive pastures, because their poor soil quality and fluctuating water regime makes them unsuitable for intensive agriculture and forestry. However, after the collapse of the socialist regime at the end of the 20th century, socio-economical changes resulted in a significant decrease in former livestock numbers and a large-scale abandonment of semi-natural pastures (Isselstein et al., 2005). The lack of grazing promotes litter accumulation and shrub encroachment on pastures, leading to an overall decline in their conservation values (Valkó et al., 2018). In order to mitigate the negative effects of abandonment, conservation managers seek alternative management options, such as mowing. However, we have scarce information on how arthropod assemblages are influenced by mowing in formerly grazed pastures.

Grazing and mowing can have similar effects on arthropods, including direct mortality, decreased food availability for herbivores, and reduced availability of preferred oviposition sites and diurnal refuges (O'Neill et al., 2008; Van Klink et al., 2015). However, these effects depend on many aspects of the practices applied, especially on the intensity of management. Although management is a key factor in maintaining biodiversity of semi-natural grasslands, its effect can be confounded by local factors, such as topographical features, which may enhance or mitigate the effects of management (Morris, 2000). Here, we focused on the influence of mowing in traditional salt pastures on four arthropod taxa. We also studied the possible interacting effects of management and microtopography driven vegetation patterns.

Conclusions about management effects on arthropods are often based on the responses of one taxonomic group, and less than 25% of studies have assessed more than two arthropod taxa, even though a multi-taxa approach is highly encouraged (Van Klink et al., 2015). For a better understanding of management effects on arthropods, we studied ground beetles, orthopterans, spiders and true bugs. Ground beetles and spiders are among the most abundant ground-dwelling arthropods in many terrestrial ecosystems and provide important ecosystem services such as pest control. They are widely used as indicators of environmental change, because they are highly sensitive to the alterations in their physical and biological environment (Buchholz, 2010; Kotze et al., 2011). Plant-dwelling orthopterans and true bugs generally prefer open habitats, and have remarkable functions in grassland ecosystems. They are important primary consumers and provide an abundant source of prey for many arthropods and vertebrates. Orthopterans have also received significant attention in conservation biology as their diversity is declining in many temperate regions (Steck et al., 2007). True bugs compose a highly diverse group according to their trophic behaviour, offering a special opportunity for examining the response of species with different degrees of host plant specialization (Torma and Császár, 2013).

Species richness and abundance are the most widely used measures of biodiversity conservation. Moderate disturbances by extensive management practices can promote arthropod biodiversity; however, modification and intensification of management practices generally decrease the species richness and abundance of many arthropods (Littlewood et al., 2012; O'Neill et al., 2008; Uchida et al., 2016; Van Klink et al., 2015). Changes in community composition and the resulting shift in the morphological or ecological traits of species may also be an important outcome of changes in management practices (Birkhofer et al., 2015; Dziock et al., 2011; Simons et al., 2016). In disturbed habitats, arthropods generally experience a decrease in their body size (Simons et al., 2016), and an increase in their mobility (Dziock et al., 2011; Gobbi and Fontaneto, 2008; Simons et al., 2016). With increasing land use intensity, assemblage structure of herbivores can shift towards less specialized phytophagous species (Simons et al., 2016; Torma and Császár, 2013). Beyond the analysis of changes in species diversity a functional approach has become increasingly favoured for analysing the feasibility of biodiversity conservation measures (Gobbi and Fontaneto, 2008; Perović et al., 2015; Simons et al., 2016).

In the present study, the (i) species richness, (ii) abundance and (iii) functional diversity of arthropods, as well as (iv) the community-weighted mean values of the selected traits were assessed using complementary sampling methods, and compared between management and vegetation types in replicated sites. The following traits were selected: trophic behaviour, dispersal ability and body size. We addressed the following questions: (1) Are the species richness, abundance and functional diversity of arthropods lower in mown sites than in grazed ones? (2) Does the community-weighted mean value of the species traits differ between mown and grazed sites? (3) Do the microtopography driven differences in the vegetation and the possible interaction between mowing and vegetation type influence the arthropod assemblages? (4) Do the effects of mowing and vegetation type vary between the different arthropod taxa?

2. Materials and methods

2.1. Study regions

The present study was carried out in three grasslands in the Great Hungarian Plain, Hungary (Fig. 1, Table 1). Two grasslands were selected in the Borsodi-Mezőség region, and one in the South Tisza Valley region. These regions are floodplain lowlands formed by the River Tisza. However, the major works of the so-called "regulation of the Tisza" in the 19th century used dikes to divide the historical floodplains into flooded and non-flooded parts. The studied grasslands are located in the non-flooded parts. The study regions have a temperate continental climate characterized by warm and dry summers with at least one month of drought in the summer, and cold winters. The mean annual temperature of the Borsodi-Mezőség region is between 9.8 and 9.9 °C, and 17.2 and 17.6 °C in the vegetation period from March to November. The annual precipitation ranges between 540 and 560 mm, of which 320–330 mm falls in the vegetation period. The mean annual temperature of the Southern Tisza Valley region is between 10.4–10.6 °C and 17.6 °C in the vegetation period. The annual precipitation ranges from 510 to 540 mm of which 320 mm falls in the vegetation period (Dövényi, 2010).

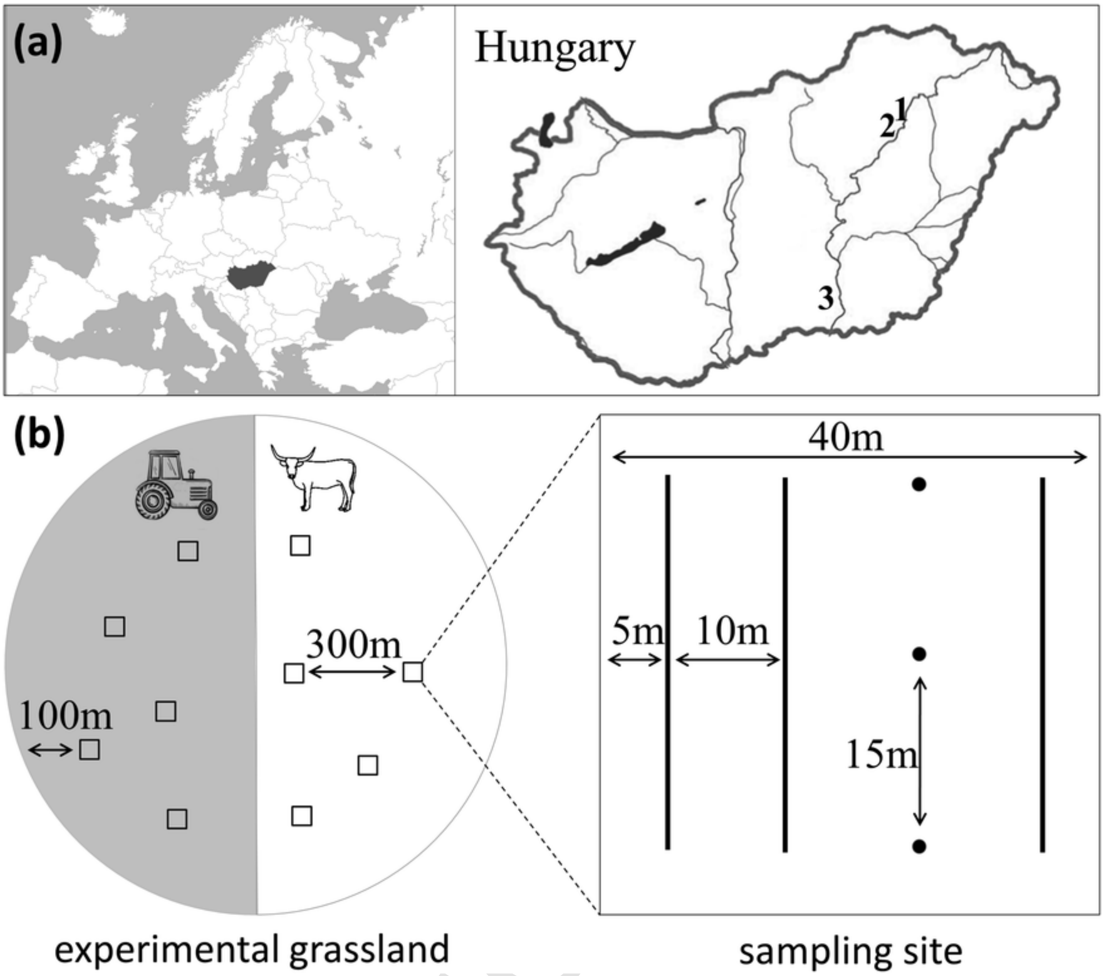

Fig. 1. The location of the grasslands studied (a) marked with numbers, and the sampling design (b). Each grassland was divided into two management units: mowing (gray part of the circle) and grazing (white part of the circle). In each management unit five 40 × 40 m sites (white squares) within a homogeneous vegetation patch were selected for sampling. At each site three pit-fall traps (black circles) were installed, and sweep-netting was carried out along three 30 m long transects (black lines).

Table 1
Geocoordinate and area (in hectare) of sampled grasslands. The numbers indicate the grasslands as shown in Fig. 1. The table also shows the number of selected salt steppe / salt meadow sites and the mean distance ± SE (in meter) between sampling sites within management units.

Grassland	Geocoordinate	Area (ha)		Number of steppe / meadow sites	Distance (m)
1	N 47° 43' 45.94"	Grazed	112	3 / 2	672 ± 78
	E 20° 48' 03.40"	Mown	126	3 / 2	590 ± 64
		Total	238		
2	N 47° 42' 37.62"	Grazed	73	2 / 3	568 ± 81
	E 20° 48' 05.64"	Mown	69	2 / 3	483 ± 47
		Total	142		
3	N 46° 21' 32.75"	Grazed	121	2 / 3	511 ± 49
	E 20° 07' 36.49"	Mown	72	2 / 3	308 ± 30
		Total	193		

2.2. Studied grasslands

Constant management regime and identical starting conditions of sampled sites are important for assessing management effects (Van Klink et al., 2015). For studying the effect of mowing in traditionally grazed grasslands, we selected those grasslands which had been managed by both grazing and mowing in a constant way for a relatively long time. Since 2004, studied grasslands have been characterized by identical management practices as all of them were divided into two management units: extensive grazing management (less than 0.5 cattle per hectare) has been continued in one part, while annual late cutting (mowing by machinery once a year in midsummer) has been established in the other part. The area of the grasslands ranged from 142 to 238 ha, and the different management units within each grassland covered an almost equal area (Table 1). Fertilizers were never applied.

2.3. Study sites and sampling

Five sites were selected in each management unit within the three grasslands, resulting in a total of 30 sampling sites (Fig. 1). We kept a distance of ca. 300 m between sites within the management units, and a distance of 100 m from the grassland edge, to decrease the spatial autocorrelation and to avoid possible edge effects, respectively. Implemented Mantel tests did not show correlations between Bray-Curtis similarities of assemblages and the distance between sites within management units. Because of the mosaic habitat structure of the salt grasslands, i.e. a distinct vegetation patch can be developed on a very small area, for sampling we selected 40 × 40 m sites within visually homogeneous vegetation patches with a minimal area of ca. 0.5 ha. Based on the dominant and characteristic plant species, we distinguished salt meadow and salt steppe patches. Salt meadow patches situated in lower elevations were characterized by the dominance of *Agrostis stolonifera*, *Alopecurus pratensis*, *Beckmannia eruciformis*, *Elymus repens* and *Puccinellia* species. Characteristics dicots were *Inula britannica*, *Lythrum virgatum*, *Rumex stenophyllus* and the endemic *Cirsium brachycephalum*. Salt steppe patches situated in higher elevations were characterized by the dominance of *Festuca pseudovina*. Characteristic salt-tolerant dicot species were *Artemisia santonicum*, *Camphorosma annua*, *Limonium gmellini* subsp. *hungarica* and *Podospermum canum*. The average height of vegetation was also recorded in six 1 × 1 m quadrats at each site before mowing. Vegetation height is generally used as an important structural index of the vegetation (e.g. Schwab et al., 2002). Prior to analyses, we tested the potential relationships between vegetation height and management, as well as the potential difference in vegetation height between meadow and steppe patches. There was no significant difference in the average height of vegetation between mown and grazed meadow sites (Mann-Whitney test: $P = 0.493$; $N = 8$, mean rank = 3.88 and $N = 8$, mean rank = 4.61 for mown and grazed sites, respectively), nor between mown and grazed steppe sites (Mann-Whitney test: $P = 0.440$; $N = 7$, mean rank = 3.29 and $N = 7$, mean rank = 4.21 for mown and grazed sites, respectively). We found a significant difference in the average height of vegetation between the steppe and meadow sites (Mann-Whitney test: $P < 0.0001$; $N = 14$, mean rank = 3.8 and $N = 16$, mean rank = 11.7 for steppe and meadow sites, respectively).

For further analyses, the vegetation type, i.e. meadow or steppe, was considered as a proxy for micro-topography driven differences in humidity and vegetation structure. These differences are often highlighted in salt grasslands (e.g. Tóth, 2010; Deák et al., 2014b). Salt meadows are generally situated in low-lying depressions characterized by moist habitat conditions and moderate or low soil salt content. The vegetation of salt meadows is generally tall and dense, producing high plant biomass, but species-poor (Deák et al., 2014b; Tóth, 2010). Salt steppe patches can develop in higher elevated areas, and are typical dry habitats with moderate or low soil salt content (Deák et al., 2014a).

Orthopterans and true bugs were sampled by sweep nets with a diameter of 40 cm. Sweeping is a generally used method to sample plant-dwelling arthropod assemblages (e.g. Torma et al., 2014). We carried out 3 × 50 sweeps per site along constant paths. At each site, three ca. 30 m long paths ran parallel to each other (Fig. 1). Sweeping was carried out between 31 May and 2 June, and 30 June and 1 July 2015.

Ground-dwelling spiders and ground beetles were sampled using funnel pitfall traps applied with a roof. Using this type of trap, the accidental catching of vertebrates can be avoided without a significant negative effect on the capture efficiency of ground beetles and spiders (Császár et al., 2018). Three traps per site were placed in a line, with an inter-trap distance of 15 m (Fig. 1). The traps were 500 ml white plastic cups with transparent plastic funnels (85 and 24 mm in upper and lower diameter, respectively). The roofs were made of white plastic plates held ca. 3–5 cm above the surface. We used 50% ethylene-glycol dissolved in water as a preservative and a few drops of odourless detergent to break the surface tension. Traps were open for two weeks in two periods before mowing (20 May – 3 June and 19 June – 2 July) in 2015.

Only the adult specimens were identified for species level by experts (true bugs by A. Torma, orthopterans by M. Bozsó, ground beetles by P. Császár and spiders by R. Gallé). The collected material was deposited in the Department of Ecology, University of Szeged.

2.4. Species traits

For the functional diversity analyses, four functional traits were considered: body size, dispersal ability, trophic guild and feeding specialization (exclusively for herbivorous true bugs). Body size was given as a continuous variable and defined as the mean body length in mm averaged over males and females. Dispersal ability was defined differently for the taxa. For true bug and ground beetle species, this was based on wing polymorphism (Gossner et al., 2015), and species were assigned into five categories with the fallowing trait values: 1 for macropterous species, 0.75 for predominantly macropterous species, 0.5 for equally shortened-winged and macropterous species (including sexual dimorphism), 0.25 for predominantly shortened-winged species and 0 for always shortened-winged species. Orthopteran species were assigned into three categories based on the mobility index (Reinhardt et al., 2005): 1 for mobile species, 0.5 for intermediate dispersers and 0 for sedentary species. Spider species were assigned into three categories based on the ballooning behaviour of the species (Blandenier, 2009). The following trait values were used: 1 for species known to balloon (species included in lists of ballooning spiders), 0.5 for spiders likely to balloon (genus included in lists) and 0 for spiders not likely to balloon (not included in lists). Species, except for spiders, were classified on the basis of trophic guilds into three categories, and the following trait values were used: 1 for carnivorous species, 0.5 for zoophytophagous, omnivorous species and 0 for phytophagous, granivorous species. Herbivorous true bug species were sorted into three categories according to their feeding specialization, and the following trait values were used: 1 for polyphagous species, 0.5 for oligophagous species and 0 for monophagous species. Trait data was collected from various literature sources and completed using the authors' previously collected databases (Appendix A).

2.5. Data analyses

The functional diversity of the four taxonomic groups was assessed by the Rao's quadratic entropy (RaoQ) multitrait index. To reveal the pattern of different trait groups, a community weighted mean (CWM) approach was used. These methods have been widely used in community-level studies and provide complementary information (e.g. Perović et al., 2015). CWM summarizes shifts in mean trait values within communities due to environmental selection for certain traits, whereas RaoQ reveals patterns of trait convergence or divergence compared to a random expectation (Ricotta and Moretti, 2011). CWM and RaoQ were computed using the FD package (Laliberté and Shipley, 2010) in R statistical environment (R Development Core Team, 2013).

To detect possible differences in species richness, abundance (activity-density in case of ground-dwelling arthropods), functional diversity and mean trait values, we applied generalized linear mixed models (GLMMs) using the R package lme4 (Bates et al., 2013). Management practice (grazing vs. mowing) and vegetation type (steppe vs. meadow) and their interaction were used as the independent variables, and grasslands nested in regions was used as random effect. We used a Poisson model for species richness, and in cases of overdispersion - typical of abundance and activity-density data - we used a negative binomial model. We used a Gaussian error term for RaoQ and CWM trait values.

We applied the indicator value analysis (IndVal) to identify characteristic species (Dufrêne and Legendre, 1997) of the different vegetation types and management regimes. The statistical significance of the species indicator values was evaluated by a Monte Carlo procedure

Table 2
The effects of management i.e., grazing (G) versus mowing (M), vegetation i.e., salt steppe (S) versus salt meadow (M) and their interaction on true bug assemblages, according to the GLMMs. Significant results are marked in bold.

	Variables	Estimated parameter (SE)	z or t value	p valu
species richness	management (G/M)	−0.3027 (0.132)	−2.285	**0.022**
	vegetation (S/M)	−0.004 (0.120)	−0.034	0.973
	management × vegetation	−0.001 (0.182)	−0.004	0.997
abundance	management (G/M)	−0.534 (0.225)	−2.371	**0.017**
	vegetation (S/M)	0.369 (0.221)	1.668	0.095
	management × vegetation	−0.469 (0.311)	−1.508	0.131
RaoQ	management (G/M)	−1.230 (0.347)	−3.537	**0.002**
	vegetation (S/M)	−0.794(0.339)	−2.339	**0.028**
	management × vegetation	0.926 (0.476)	1.945	0.066
size	management (G/M)	−0.010 (0.027)	−0.379	0.708
	vegetation (S/M)	−0.050 (0.026)	−1.864	0.074
	management × vegetation	0.024 (0.037)	0.657	0.517
dispersal ability	management (G/M)	0.195 (0.051)	3.789	< **0.0**
	vegetation (S/M)	0.0127 (0.050)	0.254	0.802
	management × vegetation	0.054 (0.070)	0.777	0.444
trophic level	management (G/M)	−0.059 (0.024)	−2.429	**0.023**
	vegetation (S/M)	−0.044 (0.0235)	−1.868	0.074
	management × vegetation	0.037 (0.033)	1.111	0.278
host plant specialization	management (G/M)	−0.039 (0.033)	−1.196	0.243
	vegetation (S/M)	0.013 (0.032)	0.428	0.672
	management × vegetation	0.005 (0.045)	0.130	0.897

with 5000 permutation. The analyses were carried out using R packege labdsv (Roberts, 2016) .

3. Results

3.1. Diversity and functional patterns of plant-dwelling arthropods

3.1.1. True bug assemblages

We collected 4416 individuals of 103 true bug species (Appendix A). The most abundant species were *Conostethus hungaricus* Wagner, 1941 and *Amblytylus nasutus* (Kirschbaum, 1856) (13.9 and 12.4%, respectively). *Myrmus miriformis* (Fallén, 1807) and *Acetropis carinata* (Herrich-Schäffer, 1841) were collected with a frequency above 5%.

Management was the main influencing factor for true bug assemblages (Table 2). Both species richness and abundance of true bugs were significantly lower in mown sites than in grazed ones (Fig. 2). The functional diversity (RaoQ) of true bugs was lower in mown sites and in meadow sites compared to grazed sites and steppe sites, respectively. The CWM of the trophic guild was lower, whilst the CWM of dispersal ability was higher in mown sites (Fig. 4).

We identified five characteristic species in grazed sites, namely *Aelia rostrata* Boheman, 1852 (0.75, p = 0.001), *A. nasutus* (0.73, p = 0.035), *Chorosoma schillingii* (Schilling, 1829) (0.63, p = 0.048), *Nabis pseudoferus* Remane, 1949 (0.77, p = 0.006) and *Stenodema calcarata* (Fallén, 1807) (0.84, p = 0.002). Except for the predaceous *N. pseudoferus*, other species are common, grass-feeding true bugs. In salt steppe patches *Berytinus crassipes* (Herrich-Schäffer, 1835) (0.44, p = 0.046) and *Capsus ater* (Linnaeus, 1758) (0.43, p = 0.014) were identified as characteristic species. We did not detect characteristic species in mown and meadow sites.

3.1.2. Orthopteran assemblages

A total of 1360 individuals of 24 orthopteran species were collected (Appendix A). The most abundant species were *Chorthippus oschei* Helversen, 1986 (19.8%), *Euchorthippus declivus* (Brisout de Barneville, 1848) (33.1%) and *Pseudochorthippus parallelus* (Zetterstedt, 1821) (24.4%).

Similarly to true bugs, orthopterans were affected by management (Table 3). Significant differences in the species richness of orthopterans were not found; however, their abundance was significantly lower in

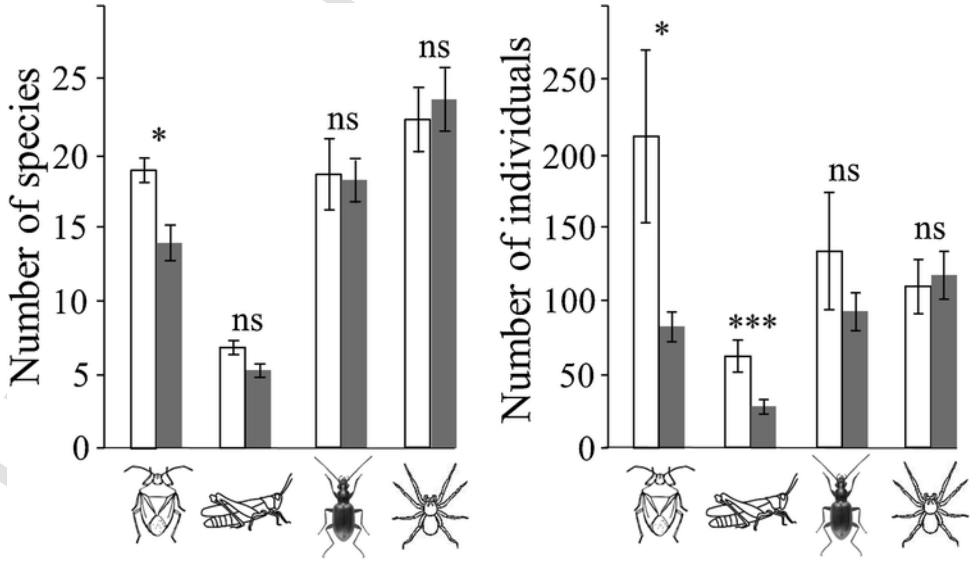

Fig. 2. Differences in the number of species (left) and individuals (right) of studied arthropod assemblages between mown sites (white bar charts) and grazed sites (gray bar charts) delineated by the GLMMs (Table 2). Bar charts indicate the mean ± SE. Significances are marked with stars: * 0.05, ** 0.01, *** 0.001.

Table 3
The effects of management i.e., grazing (G) versus mowing (M), vegetation i.e., salt steppe (S) versus salt meadow (M) and their interaction on orthopteran assemblages, according to the GLMMs. Significant results are marked in bold.

	Variables	Estimated parameter (SE)	z or t value	p value
species richness	management (G/M)	−0.325 (0.210)	−1.549	0.121
	vegetation (S/M)	−0.251 (0.198)	−1.267	0.205
	management × vegetation	0.168 (0.299)	0.561	0.575
abundance	management (G/M)	−0.901 (0.284)	−3.173	**0.001**
	vegetation (S/M)	−0.352 (0.278)	−1.267	0.205
	management × vegetation	0.275 (0.39)	0.701	0.483
RaoQ	management (G/M)	0.010 (0.336)	0.030	0.976
	vegetation (S/M)	−0.041 (0.325)	−0.127	0.900
	management × vegetation	−0.009 (0.460)	−0.021	0.983
size	management (G/M)	−0.026 (0.009)	−2.810	**0.010**
	vegetation (S/M)	−0.004 (0.013)	−0.293	0.772
	management × vegetation	−0.001 (0.019)	−0.056	0.955
dispersal ability	management (G/M)	−0.028 (0.031)	−0.909	0.372
	vegetation (S/M)	0.005 (0.030)	0.174	0.863
	management × vegetation	0.026 (0.042)	0.627	0.536
trophic level	management (G/M)	0.063 (0.041)	1.525	0.140
	vegetation (S/M)	0.025 (0.040)	0.637	0.531
	management × vegetation	−0.019 (0.057)	−0.347	0.731

Table 4
The effects of management i.e., grazing (G) versus mowing (M), vegetation i.e., salt steppe (S) versus salt meadow (M) and their interaction on ground beetle assemblages, according to the GLMMs. Significant results are marked in bold.

	Variables	Estimated parameter (SE)	z or t value	p value
species richness	management (G/M)	−0.261 (0.137)	−1.901	0.058
	vegetation (S/M)	0.518 (0.127)	4.064	**<0.001**
	management × vegetation	−0.452 (0.175)	−2.574	**0.010**
activity-density	management (G/M)	0.454 (0.319)	1.421	0.155
	vegetation (S/M)	1.1023 (0.315)	3.500	**<0.001**
	management × vegetation	−0.958 (0.438)	−2.186	**0.028**
RaoQ	management (G/M)	−0.010 (0.008)	−1.255	0.221
	vegetation (S/M)	−0.000 (0.007)	−0.073	0.941
	management × vegetation	0.016 (0.011)	1.426	0.166
size	management (G/M)	−0.044 (0.038)	−1.149	0.261
	vegetation (S/M)	−0.007 (0.037)	−0.205	0.839
	management × vegetation	0.042 (0.052)	0.809	0.426
dispersal ability	management (G/M)	0.033 (0.074)	0.449	0.657
	vegetation (S/M)	−0.002 (0.072)	−0.025	0.980
	management × vegetation	−0.044 (0.102)	−0.429	0.671
trophic level	management (G/M)	0.051 (0.096)	0.533	0.599
	vegetation (S/M)	0.276 (0.093)	2.938	**0.007**
	management × vegetation	−0.104 (0.131)	−0.793	0.435

mown sites than in grazed ones (Fig. 2). The CWM of body size was also negatively related to mowing (Fig. 4).

E. declivus (0.69, p = 0.023) and *Platycleis affinis* Fieber, 1853 (0.37, p = 0.048) were characteristic species in grazed sites, but we did not detect characteristic species in mown sites. Two subxerophilous species, *E. declivus* (0.51, p = 0.047) and *Tesselana veyselli* (Koçak, 1984) (0.65, p = 0.008) were found as characteristic species in salt steppe sites.

3.2. *Diversity and functional patterns of ground-dwelling arthropods*

3.2.1. *Ground beetle assemblages*

Altogether, 3394 individuals of 98 ground beetle species were collected (Appendix A). The most abundant species was *Carabus cancellatus* (Illiger, 1798) (17.5%). Besides this species, *Agonum viridicupreum* (Goeze, 1777), *Brachinus elegans* (Chaudoir, 1842), *Chlaenius festivus* (Panzer, 1796), *Harpalus rubripes* (Duftschmid, 1812) and *Microlestes minutulus* (Goeze, 1777) were collected with a frequency above 5%.

Management was not a significant main effect for ground beetles in contrast to vegetation type (Table 4). However, the significant interaction between management and vegetation type indicated that the species richness and activity-density of ground beetles responded negatively to mowing in salt meadow sites. In salt meadow sites significantly more species and individuals were collected (Fig. 3), and the CWM of trophic guild was higher than in salt steppe sites (Fig. 4).

In meadow sites many carnivorous species with preferences for wet habitats such as *A. viridicupreum* (Goeze, 1777) (0.44, p = 0.015), *Amblystomus niger* (Heer, 1841) (0.42, p = 0.021), *Badister bullatus* (Schrank, 1798) (0.40, p = 0.016), *Brachinus explodens* (Duftschmid, 1812) (0.42, p = 0.013), *B. nigricornis* (Gebler, 1829) (0.43, p = 0.044), *Pterostichus vernalis* (Panzer, 1796) (0.39, p = 0.049), *Syntomus obscuroguttatus* (Duftschmid, 1812) (0.56, p = 0.019) and *Trechus quadristriatus* (Schrank, 1781) (0.41, p = 0.042) were detected as characteristic species. In steppe sites, the drought-tolerant *Harpalus attenuatus* (Stephens, 1828) (0.50, p = 0.023) *H. flavicornis* (Dejean, 1829) (0.60, p = 0.047) and *Ophonus diffinis* (Dejean, 1829) (0.38, p = 0.050) were detected as characteristic species.

3.2.2. *Spider assemblages*

A total of 3406 individuals belonging to 109 spider species were collected (Appendix A). The most abundant species were *Hogna radiata* (Latreille, 1817) (13.8% of total catch) and *Ozyptila trux* (Blackwall, 1846) (9.5%). Several other species, such as *Metopobactrus deserticola* Loksa, 1981, *Pardosa prativaga* (L. Koch, 1870), *Phrurolithus festivus* (C. L. Koch, 1835) and *Trochosa ruricola* (De Geer, 1778) were collected with a frequency above 5%.

Management did not have any significant effects on spider assemblages (Table 5). There were significantly more individuals in meadow sites compared to steppe sites (Fig. 3). The community weighted mean body size of spiders was higher whilst the CWM of dispersal ability was lower in steppe sites than in meadow sites (Fig. 4).

Several characteristic species, typically species with preferences for wet habitats, were detected in salt meadow sites. They were *Arctosa leopardus* (Sundevall, 1833) (indval: 0.43, p = 0.050), *Ozyptila trux* (Blackwall, 1846) (0.59, p = 0.049), *Pardosa prativaga* (L. Koch, 1870) (0.60, p = 0.047), *Trochosa ruricola* (De Geer, 1778) (0.72, p = 0.027) and *Zelotes mundus* (Kulczyński, 1897) (0.57, p = 0.024). Furthermore, *Xysticus kochi* Thorell, 1872 (0.70, p = 0.002) a drought-tolerant species, was found as a characteristic species in salt steppe sites.

4. Discussion

In the present study, the taxonomic and functional diversity of arthropods were compared between mown and grazed parts of traditionally grazed salt grasslands. The number of true replications was restricted as we could select only three independent grasslands for the study. However, these grasslands provided a special opportunity for examining the possible effect of mowing as an alternative to traditional grazing managment. To the best of our knowledge our study is the first to analyse the long-term diversity and functional responses of four taxonomical groups of arthropods to mowing as an alternative to grazing

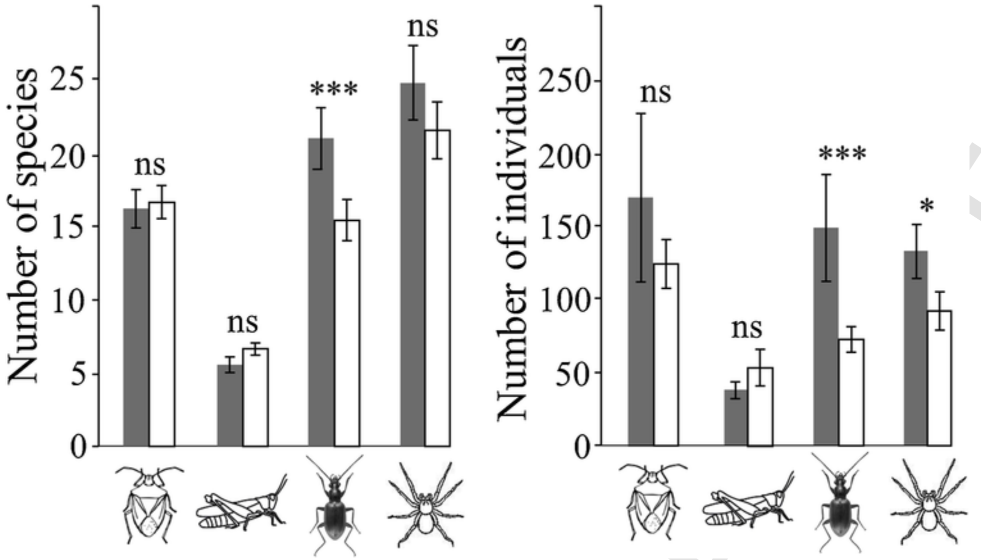

Fig. 3. Differences in the number of species (left) and individuals (right) of studied arthropod assemblages between salt steppe sites (white bar charts) and salt meadow sites (gray bar charts) delineated by the GLMMs (Table 2). Bar charts indicate the mean ± SE. Significances are marked with stars: * 0.05, ** 0.01, *** 0.001.

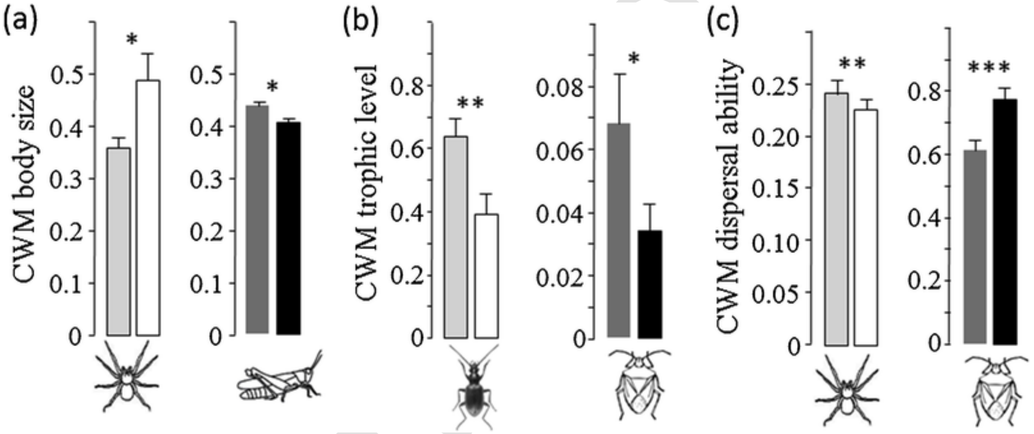

Fig. 4. Significant shifts in the community weighted mean (CWM) trait values of body size (a), trophic level (b) and dispersal ability (c) corresponding to vegetation (light gray and white charts for salt meadow and salt steppe vegetation, respectively) and management (dark gray and black charts for grazing and mowing, respectively). Bar charts indicate the mean + SE. Significances are marked with stars: * 0.05, ** 0.01, *** 0.001.

management, and the main results of the present study suggest a taxon-dependent response of arthropods. Our finding - that management was a main driver for true bug and orthopteran assemblages but not for ground-dwelling spider and ground beetle assemblages - is concordant with the suggestion that plant-dwelling species are affected most severely by the removal of the vegetation layer (Jonas et al., 2002).

4.1. *The effect of management on plant-dwelling arthropod assemblages*

Due to the removal of all vegetation at once, freshly mown meadows are unsuitable for the feeding of herbivorous species, such as the majority of true bugs and orthopterans, and cannot provide shelter from inclement weather or avian predation (Gardiner et al., 2002). Furthermore, mown sites may also be unfavourable for certain species due to the altered microclimatic conditions (Gardiner and Hassall, 2009). True bugs and orthopterans usually lay their eggs directly onto plants (Dziock et al., 2011; Martínez et al., 2013). Therefore, cutting the vegetation can directly damage eggs, and also juveniles which have a low mobility and low chance of escape. In addition, mowing machines can kill a large number of adult individuals, particularly of orthopterans as their large size and location in the vegetation may render them susceptible to direct damage by mowing machines (Gardiner and Hill, 2006; Humbert et al., 2010). These disturbances can result in reduced population sizes and decreased species richness (Di Giulio et al., 2001; O'Neill et al., 2008). In accordance with Badenhausser and Cordeau (2012), we suggest that management practices particularly influence the abundance of orthopterans. The likely reason for this is that the abundance of orthopterans is generally more sensitive to disturbances than their species richness (Löffler and Fartmann, 2017; Torma et al., 2018).

Indicator species were detected only in grazed sites underpinning the negative influence of mowing. Regarding the selected traits, mean body size of orthopterans was smaller in mown sites than in grazed sites, highlighting the negative effect of mowing on large orthopterans. Beside the potentially serious harm to large insects caused by mechanical mowing, large species also tend to have a longer life cycle and a smaller population size, which may render their development or reproduction more susceptible to being disrupted by various disturbances (Simons et al., 2016). The high mean value of the dispersal ability of true bugs in mown sites was presumably due to the different disturbance regime created by mowing and grazing. Mechanical mowing

Table 5
The effects of management i.e., grazing (G) versus mowing (M), vegetation i.e., salt steppe (S) versus salt meadow (M) and their interaction on spider assemblages, according to the GLMMs. Significant results are marked in bold.

	Variables	Estimated parameter (SE)	z or t value	p value
species richness	management (G/M)	0.075 (0.117)	0.643	0.520
	vegetation (S/M)	0.135 (0.111)	1.217	0.224
	management × vegetation	−0.024 (0.154)	−0.160	0.873
activity-density	management (G/M)	0.133 (0.137)	0.971	0.331
	vegetation (S/M)	0.300 (0.133)	2.254	**0.024**
	management × vegetation	−0.056 (0.185)	−3.040	0.761
RaoQ	management (G/M)	0.003 (0.008)	0.404	0.689
	vegetation (S/M)	0.012 (0.008)	1.492	0.148
	management × vegetation	−0.015 (0.011)	−1.291	0.208
size	management (G/M)	0.018 (0.047)	0.395	0.696
	vegetation (S/M)	−0.121 (0.048)	−2.521	**0.018**
	management × vegetation	0.001 (0.096)	0.015	0.988
dispersal ability	management (G/M)	0.019 (0.060)	0.321	0.751
	vegetation (S/M)	0.153 (0.059)	2.591	**0.016**
	management × vegetation	−0.084 (0.082)	−1.022	0.317

brings a short term but very intensive disturbance to the whole grassland at once. Good dispersal ability may be advantageous for species in the recolonization of habitats after such a disturbance, resulting in a higher average dispersal ability in disturbed habitats (Birkhofer et al., 2015; Dziock et al., 2011). Extensive grazing probably does not affect the average dispersal ability of arthropods because it results in a moderate continuous biomass removal, and a heterogeneous habitat structure (Simons et al., 2016). The lower proportion of higher trophic guilds in mown sites compared to grazed ones suggests that disturbance of the regime by mowing is disadvantageous for carnivorous true bugs. However, the observed shift in the trophic level of true bugs may be due to the *Nabis* species. These species were highly dominant among carnivorous bugs but were collected in low abundance in mown sites (e.g., *N. pseudoferus* was a significant indicator species in grazed sites), suggesting that mowing is disadvantageous for them. Horton et al. (2003) reported that even a modest decrease in mowing frequency was enough to generate significant increases in the number of *Nabis* spp.

4.2. The effect of vegetation type on plant-dwelling arthropod assemblages

Previous studies in Pannonian grasslands (Torma et al., 2014, 2017) have highlighted the importance of microtopography driven differences in shaping true bug and orthopteran assemblages, particularly by influencing vegetation patterns. Based on the results of indicator species analyses, we also suggest a general role for the difference in the moisture condition between steppe and meadow sites in shaping arthropod assemblages. However, it was somewhat surprising that vegetation type had only a weak effect on the diversity of plant-dwelling arthropods in contrast to ground-dwelling ones. Presumably, for the generalist, grass-feeder species like the majority of collected true bugs and orthopterans, both salt steppe and salt meadow patches provide suitable resources. Furthermore, changes in soil moisture presumably had less influence on plant-dwelling assemblages than ground-dwelling ones. For example, soil conditions did not have a direct influence on true bugs in contrast to e.g. ground beetles (Sanderson et al., 1995).

4.3. The effect of management on ground-dwelling arthropod assemblages

In the case of ground-dwelling arthropod assemblages, a significant interacting effect of mowing and vegetation type was found for ground beetle species richness and activity-density whilst spiders were not influenced by management. Lafage and Pétillon (2014) highlighted the difference between spiders and ground beetles in their response time to disturbances caused by cutting, and suggested that this can be explained by the high dispersal tendency of spiders over both short and long distances. Thus, spiders generally show an immediate response to management disturbances, but are less sensitive in the long term (Lafage and Pétillon, 2014), which may explain the lack of any significant management effects on spiders in the present study. The interacting effect of mowing and vegetation on ground beetles suggests a negative influence of mowing on ground beetle diversity in salt meadows, but not in salt steppes. Ground beetles seem to prefer meadow patches presumably due to the more humid microclimatic conditions and taller vegetation. Soil moisture is critical for ground beetles because eggs absorb water from their surroundings to complete embryonic development and larvae are sensitive to desiccation (Kotze et al., 2011). In humid and tall meadow vegetation, the changes in physical environmental conditions after mowing are greater than in salt steppes, which might have a negative impact on ground beetles.

Generally, management seemed to be less important for ground-dwelling arthropods than plant-dwelling ones. Presumably, the remarkable microtopography driven differences in the habitat properties can override the effect of management on ground-dwelling arthropods. Strong stressors are known to override the effect of management. For example, flooding is a more important driver for spider and ground beetle assemblages than management regime in floodplain grasslands (e.g. Lafage and Pétillon, 2016).

4.4. The effect of vegetation type on ground-dwelling arthropod assemblages

Vegetation type was found as the main driver in shaping ground-dwelling arthropod assemblages. In coastal salt marshes – a somewhat similar habitat – various researchers, e.g. Finch et al. (2007); Irmler et al. (2002); Pétillon et al. (2007), have shown that spiders and ground beetles are highly influenced by the differences in vegetation according to elevation, i.e. lower and upper marshes. Beside the differences in vegetation properties, it has also been suggested that the differences in soil and microclimatic conditions and inundation have important roles in shaping ground-dwelling arthropod assemblages (Pétillon et al., 2008).

Vegetation structure has a profound importance for generalist predators such as spiders (e.g. Buchholz, 2010) and ground beetles (e.g. Cole et al., 2006). Thus, in the humid and tall meadow vegetation the species richness and activity-density of spiders and ground beetles were higher. The observed shift in the trophic guilds of ground beetles between vegetation types can also be due to the positive effect of vegetation structure on generalist predators. Typically, in salt meadow patches characteristic species of ground beetles were carnivores with preferences for wet habitats whereas in salt steppe patches characteristic species were drought-tolerant seed predators. In the sense of moisture preference, similar pattern was found for spiders. Furthermore, the difference in moisture conditions between meadow and steppe vegetation patches suggests a negative relationship between soil moisture and the mean body size of spiders. Entling et al. (2010) demonstrated that spider body size decreased along the warm/dry to cool/moist environmental gradient at various spatial scales and suggested that soil water content is particularly important for ground-dwelling spiders. This relationship was not depended on sex (Entling et al., 2010); thus, averaging the body size across sexes in the present study presumably did not result in a methodological bias in the observed relationship between moisture condition and the mean body size of spiders. In general, larger individuals are less prone to desiccation or osmotic disruption, thus can exploit hot and dry habitats (Whitman, 2008). However, this pattern can be confounded with biotic-interactions such as predation or interference competition (Entling et al., 2010).

Salt meadows are generally covered by water in spring. Good dispersal ability may be advantageous for spiders in the recolonization of salt meadows after they dry out, resulting in the observed higher mean value of dispersal ability in salt meadow sites than in salt steppe sites. On the other hand, wind-dispersal, such as ballooning in spiders, is more typical of small species (den Boer, 1990), so the mechanism behind the observed shift in the dispersal ability of spiders may be also linked to the shift in their body size distribution.

4.5. Grazing or mowing – which is better for arthropods?

Only a few studies (e.g. McKenzie et al., 2016) have found that grazing and mowing act as similar ecological filters for arthropods. The majority of the studies have suggested that grazed and mown grasslands provide different habitat conditions for arthropods even though study results are often confusing in terms of whether mowing or grazing is the preferable management for promoting arthropod diversity. Some studies (e.g. Grandchamp et al., 2005) have suggested that grazing has fewer negative effects on ground beetles than mowing. Mowing was reported to have no effects - or if there were any, these were positive - on the species richness of both spiders and ground beetles (e.g. Pétillon et al., 2007). The majority of studies, similarly to the present study, suggested the disadvantages of mowing for Orthoptera diversity compared with grazing. (e.g. Kampmann et al., 2008; Weiss et al., 2013; but see Radlmair and Laussmann, 1997). Contradicting our results, Zurbrügg and Frank (2006) found that mown meadows and wildflower strips clearly increased the species richness of true bugs compared to extensive pastures. They suggested that the disturbance caused by the immediate removal of the vegetation cover by cutting is presumably not as great for true bug assemblages as is the more continuous disturbance caused by grazing. As is also shown by our results, the advantages and disadvantages of grazing and mowing depend on many circumstances, such as the taxonomical group studied, the vegetation type and the traditional management regime. This highlights the importance of targeted research to design locally appropriate conservation strategies.

5. Conclusions and implication for conservation

Our comprehensive analyses of the diversity and functional responses of four taxonomical groups to mowing in traditional pastures suggest the following general patterns. First of all, it seems that plant-dwelling arthropods react more sensitively to mowing than ground-dwelling arthropods. Presumably, strong stressors such as drought can partly mask the management effects on ground-dwelling arthropods, and habitat heterogeneity can achieve the same effect by influencing the gradient of these stressors. However, the effect of uniform biomass removal on large areas at once and the direct mortality caused by mowing are the most disadvantageous for plant-dwelling arthropods. We agree that it is difficult to recommend a preferable management option to support the biodiversity of semi-natural grasslands; however, our findings confirm the conclusion of Uchida et al. (2016) that for biodiversity conservation, maintaining the traditional management regime is generally the best option. Introducing a new technique can lead to a decline in biodiversity. As suggested by our results, in Pannonian salt grasslands extensive grazing seems to be the best land use type to maintain arthropod biodiversity.

Uncited reference

R Development Core Team (2013).

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2018.12.004.

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