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Positive small-scale effects of shrubs on diversity and flowering in pastures

Kleine Sträucher können den Arten- und Blütenreichtum in Weiden steigern

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Abstract

Understanding plant-plant interactions is essential in planning and implementing effective grassland management strategies. Positive and negative interactions generally co-occur in plant communities and the net effect of these interactions may depend on the disturbance regime, including grazing. Shrubs can act as biotic refuges by physically protecting neighbouring plants from herbivores. As a result, we would expect that in pastures the diversity and flowering success of plants is higher in the close vicinity of shrubs compared to the open vegetation. Nevertheless, we can also assume a competitive trade-off cost for plants that grow together with shrubs. In this study, we assessed the small-scale effects of dwarf shrubs (30–40 cm in diameter) on species density and flowering success. Specifically, we considered three types of microsites: (i) shrub interior, (ii) edge of shrub, and (iii) open pasture (more than 2 meters away from the shrub). We surveyed these three types of microsites using 10 × 10 cm sized plots both in grazed and ungrazed meadow steppe, in central Hungary. The highest species density was found at the edge of shrubs, both in grazed and ungrazed vegetation. Meanwhile, species density did not differ significantly between shrub interiors and the open pasture. However, in grazed vegetation, species flowering success was significantly higher in shrub interiors and edges than in the open pasture; no significant trend was observed for this measure in ungrazed vegetation. In contrast to previous studies, we did not detect a competitive effect of small-sized shrubs on plants in ungrazed vegetation. Our results indicate that small-sized shrubs protect other plants from herbivores and that the edge effect plays an important role for the maintenance of small-scale species diversity in pastures. Overall, our results underline the beneficial effect of biotic refuges in pastures and we suggest that retaining a sparse population of small-sized native shrubs is advantageous from a conservation point of view.

Keywords: edge effect, facilitation, grazing, meadow-steppe, plant-plant interactions, unpalatable plants

Erweiterte deutsche Zusammenfassung am Ende des Artikels

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1. Introduction

Grasslands have been exposed to large-scale land-use changes worldwide in the past century, including agricultural intensification and the decline of traditional management (DEÁK et al. 2014, WESCHE et al. 2016). In consequence, their diversity and spatial extent have decreased dramatically (BAKKER & BERENDSE 1999). From a conservation standpoint, evidence-based studies on mechanisms that shape grassland functioning and diversity have become indispensable.

Plant-plant interactions can trigger facilitative or competitive effects on target plants and are thus essential for planning and implementing effective grassland conservation and management strategies. Positive and negative interactions generally co-occur in plant communities and their net effect may depend on species traits, on the life stages of the interacting species (BOUGHTON et al. 2011, KELEMEN et al. 2015a), and on habitat characteristics such as abiotic stress or disturbance regimes (BROOKER & CALLAGHAN 1998, KELEMEN et al. 2013, TÖRÖK et al. 2014). Several authors found a maximum level of facilitation in stressed habitats with low productivity (BERTNESS & CALLAWAY 1994, KIÆR et al. 2013, KELEMEN et al. 2015b), while others found a maximum at medium productivity (MAESTRE et al. 2005, MICHALET et al. 2006, HOLMGREN & SCHEFFER 2010). Some authors also suggested that the overall effect of biotic interactions does not change along the stress gradients (TILMAN 1987, WILSON & TILMAN 1993). The balance between positive and negative plant interactions along the stress gradients is not always consistent. Several studies have suggested that the facilitative effect of unpalatable plants functioning as biotic refuges can be maximal at moderate grazing pressure (BOSSUYT et al. 2005, SMIT et al. 2009, KOYAMA et al. 2015). Unpalatable plants can physically protect co-existing plants from herbivores and can also provide favourable abiotic environment for plant performance by increasing the soil humidity and nutrient content (BOSSUYT et al 2005, HOWARD et al. 2012). The functional traits of benefactors influence the effect on beneficiary species. For example thorny shrubs can provide a more effective, long-term protection than herbaceous benefactors (REBOLLO et al. 2002, HOWARD et al. 2012, KOYAMA et al. 2015).

The protection provided by thorny shrubs can remain stable with increasing grazing pressure (REBOLLO et al. 2005, HOWARD et al. 2012). In other cases (e.g., in the case of grasses as benefactors) the protective effect can collapse with increasing grazing pressure, because livestock can destroy biotic refuges by trampling and feeding on the benefactor (KOYAMA et al. 2015). Protection by shrubs is most important for highly palatable species, for seedlings and for species with low clonal spreading and resprouting abilities (MILCHUNAS et al. 1988, BOSSUYT et al. 2005, KLIMEŠOVÁ et al. 2008, LÓPEZ-SÁNCHEZ 2016). Protection against herbivory by unpalatable plants generally results in an increased seed production by the beneficiary species, which can increase species diversity (CALLAWAY et al. 2000).

Whereas shrubs have a facilitative effect in grazed grasslands, they likely have a competitive effect in ungrazed grasslands (HOWISON et al. 2015). This competitive effect would derive from the shading caused by the shrub and the accumulated litter underneath (BOSSUYT et al. 2005). Besides the above-described biotic interactions between unpalatable shrubs and other pasture species, edges of these biotic refuges can have further functions, like being effective seed traps (RIES et al. 2004). Consequently, we would expect that in grazed conditions, the interaction of plants growing together with shrubs is a trade-off between the combined positive effects of physical protection, ambient microclimate and seed trapping, on the one hand, and a competitive effect on the other hand (BOSSUYT et al. 2005, KOYAMA et al. 2015).

Despite the high number of studies on the role of biotic refuges in pastures, there is little knowledge about the effect of unpalatable shrubs on subordinate plants depending on their position (i.e. growing beneath shrubs or in the edge of shrubs). The main goal of this study was to assess the net-effect of small-sized *Crataegus monogyna* shrubs (30–40 cm in diameter, 30–50 cm height) on the species density and flowering success in the interior and in the edge of the shrubs, under field conditions. We aimed to study the effect of this thorny shrub species because, being long-lived and unpalatable, it could act as a biotic refuge for plant species and facilitate species diversity. We specifically focused on small-sized individuals because they were very abundant in the habitat. More importantly, bigger shrubs often lose their lower branches. This way, their understorey can become available for grazing and can even attract grazers by operating as shady shelters (LÓPEZ-SÁNCHEZ et al. 2016).

2. Materials and methods

2.1 Study area and sampling

The study area was located in the central part of the Great Hungarian Plain, in the Kiskunság National Park (47°06'N, 19°16'E). This region is characterized by a continental climate; the mean annual temperature is 10 °C and the mean annual precipitation sum is 520 mm (VADÁSZ et al. 2016). Pristine grasslands cover several thousand hectares; most of them are species-rich meadow steppes originated from *Molinia* meadows (*Molinion coeruleae* Koch 1926) and are dominated by *Molinia caerulea*, *Chrysopogon gryllus*, *Poa angustifolia* and *Agrostis stolonifera* (MOLNÁR et al. 2008, VADÁSZ et al. 2016). This habitat type has a high conservation value due to its high diversity and unique species pool encompassing several orchid species (e.g., *Anacamptis pyramidalis*, *Ophrys sphegodes*, *Orchis coriophora*) and several other plants protected in Hungary (e.g., *Centaurea scabiosa* subsp. *sadleriana*, *Gentiana pneumonanthe*, *Iris sibirica*, *Iris spuria*, *Koeleria javorkae*, *Ophioglossum vulgatum*, *Schoenus nigricans*, *Veratrum album*).

The studied meadow steppe was divided into two adjacent sites, managed differently in the study year, giving an opportunity to use split-plot design during the sampling. The studied sites represented different paddocks (grazing units): a grazed unit and a unit that was ungrazed in the year of sampling. Both units had been managed by extensive beef cattle grazing for decades. Medium grazing intensity is typical in our study sites from April to November, with 0.3–0.5 animal unit/ha. Based on the experience of local conservation managers, the estimated age of *Crataegus monogyna* individuals ranged between 5 and 25 years, but usually they remained small-sized as their buds and young leaves had been removed periodically by domestic cattle and wild Roe Deer (*Capreolus capreolus*). In the present study we focused on the effect of small-sized *Crataegus monogyna* shrubs, which were 30–50 cm tall and had an approximate canopy diameter of 30–40 cm (Fig. 1).

Both in grazed and ungrazed units, we surveyed the following three types of microsites using 10 × 10 cm sized plots: (i) shrub interior, (ii) edge of shrub and (iii) open pasture (control). The shrubs were selected randomly and the plots were arranged as follows: a 3 × 3 grid of nine plots was placed underneath a shrub (shrub interior), 12 plots were aligned along the edges of the grid, coinciding with the margin of the dense shrub canopy (edge of shrub; Fig. 2). The control plots followed an identical plot design and were placed in the open pasture, more than two meters away from the shrub (Fig. 2). We defined a plot type as the combination of microsite type and grazing unit (e.g., shrub interior in grazed unit) and plot group as all particular plots at a shrub and all of the three grids in the open pasture (control). In total, eleven plot groups (eight groups with a shrub and three control plot groups) were placed in the grazed and the ungrazed units, respectively (Fig. 2). Therefore, our sampling setup consisted of altogether 462 plots with the following distribution: 2 (grazed and ungrazed units) × 8 (plot groups per unit) × 9 (plots per replicate) plots in the shrub interior, 2 × 8 × 12 plots at the edge of

Fig. 1. Small-sized *Crataegus monogyna* shrub as a biotic refuge for other plant species in the study area. (Photo: A. Kelemen, 20 June 2015).

Abb. 1. Kleinwüchsiger *Crataegus monogyna*-Strauch als biotisches Refugium für andere Pflanzenarten im Untersuchungsgebiet. (Foto: A. Kelemen, 20.06.2015).

shrubs and 2 × 3 × 21 in the open pasture. We recorded the occurrences (presence-absence) of all vascular plant species and also the presence-absence data of their reproductive organs (flower or fruit) in each plot. The field survey was conducted at the end of June 2015, during peak flowering.

2.2 Data analyses

To explore the similarities between the species composition across plot types, we used PCA ordination based on the relative frequency of species. The ordination was performed using the "vegan" package (OKSANEN et al. 2017) in R (R CORE TEAM 2016).

Species density and the number of flowering species (dependent variables) did not follow normal distributions. Consequently we performed generalized linear models (GLM) with a Poisson distribution. We tested the effects of grazing unit (i.e. grazed, ungrazed), microsite type and their interactions as fixed factors on species density and the number of flowering species. We tested the significance of predictors through backward removal and calculation of the Wald statistics. In addition, we used Mann-Whitney U tests with continuity corrections to analyze differences in the dependent variables between the microsite types (ZAR 1999).

Moreover, we introduced an index to describe the relative flowering success (RFS) using the following formula at plot type level:

$$\text{RFS}=\frac{\frac{1}{n}\sum_{ijk}^{n}\frac{fijk}{pijk}}{\frac{1}{N}\sum_{i}^{N}\frac{Fi}{Pi}},$$

where *n* is the number of species in the particular plot type of the certain plot group, N is the total species number detected in the whole study, *fijk* is the number of plots within the particular plot type of the certain plot group where the *i*th species produced flower or fruit, *pijk* is the number of plots within

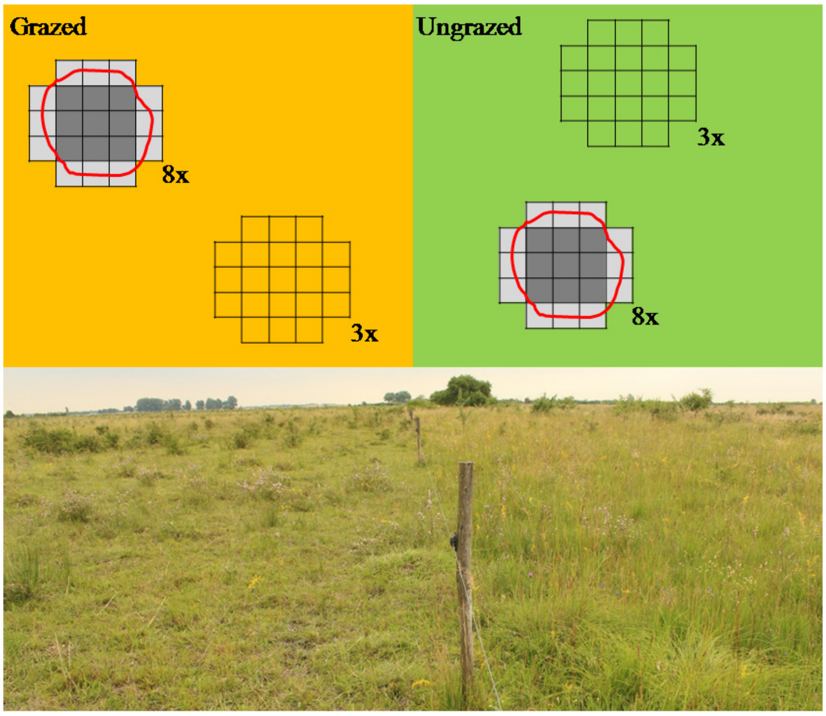

Fig. 2. Sampling design and the studied pasture divided into two adjacent sites (i.e. grazed and ungrazed). Red lines represent the edge of the dense canopy of shrubs. Dark grey plots – shrub interior; light grey plots – edge of shrub; open plots – control.

Abb. 2. Muster der Probenahme und die untersuchte, in zwei benachbarte Flächen (beweidet und unbeweidet) unterteilte Weide. Rote Linien stellen den Rand der dichten Überschirmung durch Sträucher dar. Dunkle graue Plots – Strauchinneres; helle graue Plots – Strauchrand; offene Plots – Kontrolle.

the particular plot type of the certain plot group where the *i*th species occurred, *Fi* is the total number of plots where the *i*th species produced flower or fruit, *Pi* is the total number of plots where the *i*th species occurred. The quotient *fijk/pijk* was calculated for every species within the particular plot type of the certain plot group and then averaged, whereas the quotient *Fi/Pi* was calculated across species and then averaged. In this calculation, we only considered species with detected flowering event in any of the plots (species with $Fi > 0$). If the value of this index is 1, the average probability of flowering of species in the particular plot type is equal to the expected probability of flowering of these species considering all plots (as a null model). If the value of this index is > 1, the flowering of the species in the particular plot type is more probable than expected by chance and if this index is < 1 it is less probable. We also calculated species preference indices at plot type level using the following method: we divided the probability of species occurrence in a particular plot type of a certain plot group with the probability of occurrence in all of the surveyed plots. We tested this preference in 15 species that achieved the highest frequencies (more than 60 occurrences in our 462 plots) and that occurred in every plot type.

The above-mentioned two indices provide data at plot type level for each plot group thus a GLM analysis was not possible. Therefore we used Kruskal-Wallis tests to reveal the significant differences ($p < 0.05$) between plot types. Then we performed Mann-Whitney U tests with continuity corrections to compare the relative flowering success and species preference indices in different plot types (ZAR 1999). All of the above-mentioned calculations, except for the PCA ordination, were performed using STATISTICA 10.0 (StatSoft Inc., Tulsa). Species nomenclature follows KIRÁLY (2009).

3. Results

There were no considerable differences in species composition between plot types. Their convex hulls widely overlapped in the PCA ordination (Fig. 3).

Species density per plot was significantly affected by grazing unit ($W = 5.47$, $p = 0.019$) and microsite type ($W = 25.03$, $p < 0.001$), but the effect of their interaction was not significant ($W = 2.37$, $p = 0.305$; Fig. 4A). Species density was higher at the edge of shrubs (means: 7.8 for grazed and 9.0 for ungrazed units) than in shrub interiors (means: 6.9 for grazed and 7.1 for ungrazed units) and open control plots (mean: 7.0 for grazed and 7.5 for ungrazed units), while the species density of the latter two microsite types did not differ significantly. Species density reached its maximum in the ungrazed unit, at the edge of shrubs; nevertheless, there were similar trends in the grazed and in the ungrazed meadow steppes (Fig. 4A).

The number of flowering species was significantly affected by the grazing unit ($W = 37.33$, $p < 0.001$) and the microsite type (Wald stat = 16.72, $p < 0.001$), and also by their interaction (Wald stat = 11.05, $p = 0.004$) (Fig. 4B). In the grazed unit, the number of flowering species did not differ significantly in the shrub interiors and at the edges, but it was significantly lower in open vegetation than in the previous two microsite types. In the

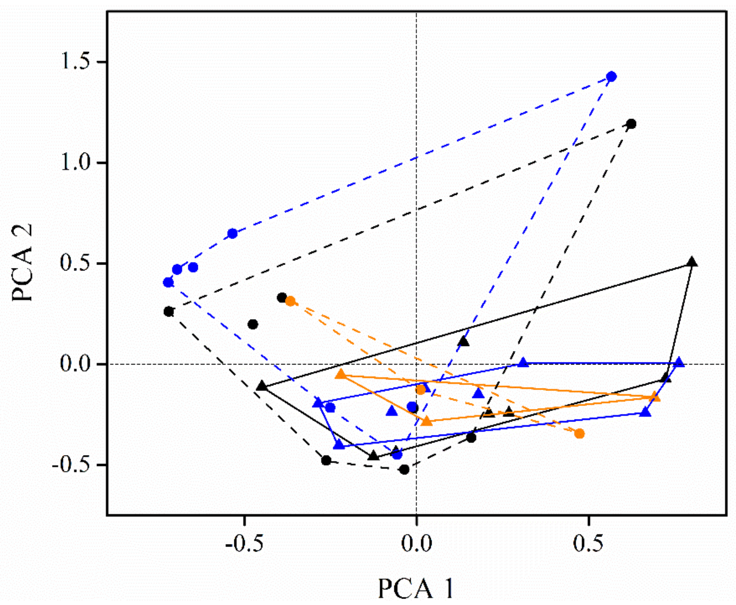

Fig. 3. PCA ordination based on the relative frequency of species in the different plot types. Grazed unit – continuous line and triangles; ungrazed unit – dashed line and circles. Colours: Black – shrub interior; blue – edge of shrub; orange – open vegetation. Eigenvalues for 1st and 2nd axis: 0.252 and 0.169; explained variation: 9% and 7.1%, respectively.

Abb. 3. PCA-Ordination basierend auf der relativen Frequenz von Arten in den unterschiedlichen Plot-Typen. Beweidete Einheit – durchgehende Linie und Dreiecke; unbeweidete Einheit – gestrichelte Linie und Kreise. Farben: Schwarz – Strauchinneres, blau – Strauchrand; orange: offene Vegetation. Eigenwerte für 1. und 2. Achse: 0,252 and 0,169. Erklärte Variation: 9 % bzw. 7,1 %.

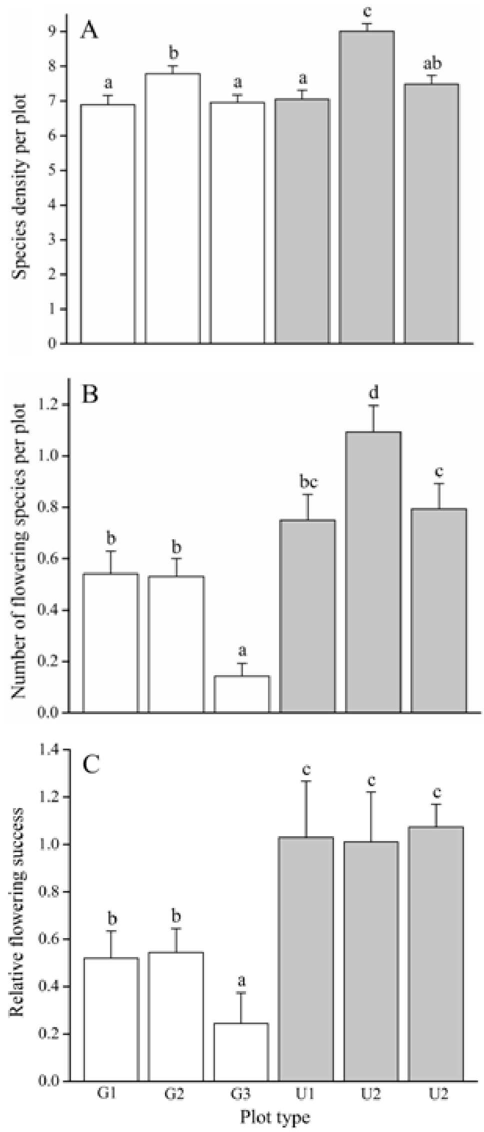

Fig. 4. Species density **A)** number of flowering species, **B)** and relative flowering success, **C)** in different plot types (mean + SE). Notations: white bars – grazed unit; grey bars – ungrazed unit; G1 – grazed shrub interior; G2 – grazed shrub edge; G3 – grazed control; U1 – ungrazed shrub interior; U2 – ungrazed shrub edge; U3 – ungrazed control. Different letters denote significant differences obtained with Mann-Whitney U tests ($p < 0.05$).

Abb. 4. Artendichte **A)** Anzahl der blühenden Arten, **B)** und relativer Blüherfolg, **C)** in unterschiedlichen Plot-Typen (Mittelwert + SD). Erläuterung: weiße Säulen – beweidete Einheit; graue Säulen – unbeweidete Einheit; G1 – beweidetes Strauchinneres; G2 – beweideter Strauchrand; G3 – beweidete Kontrolle; U1 unbeweidetes Strauchinneres; G2 – unbeweideter Strauchrand; G3 – unbeweidete Kontrolle. Unterschiedliche Buchstaben bezeichnen signifikante Unterschiede nach Mann-Whitney U-Tests ($p > 0{,}05$).

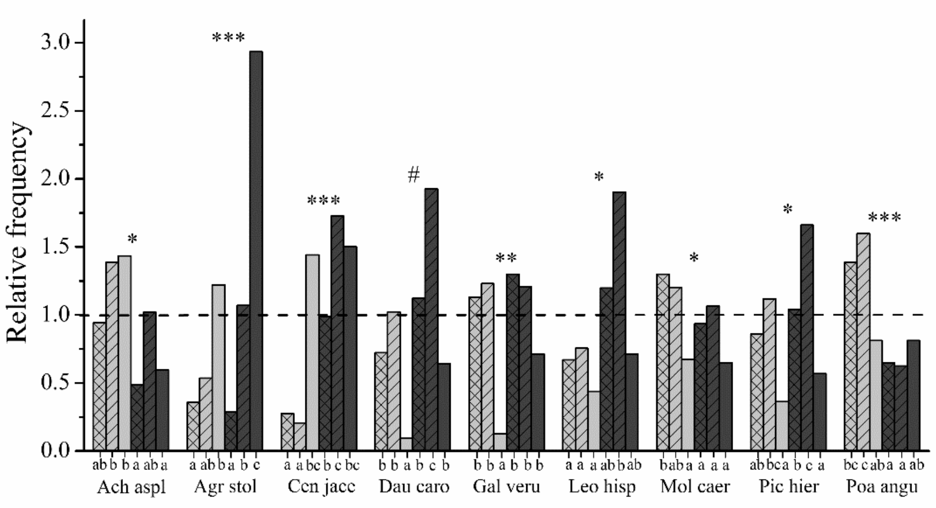

Fig. 5. Probability of species occurrence in different plot types compared with the probability of occurrence in the all of surveyed plots (i.e. relative frequency of species in the particular plot type). Notations: light columns – grazed unit; dark columns – ungrazed unit, columns with crossed lines – shrub interior, columns with parallel lines – shrub edge, columns without lines – open vegetation. Asterisks denote the results of a Kruskal-Wallis test for each species, with significance levels: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, $^{\#}p < 0.1$ (marginally significant). Different letters within a column group denote significant pairwise-differences obtained with Mann-Whitney U tests ($p < 0.05$).

Abbreviations: Ach aspl: *Achillea asplenifolia*, Agr stol: *Agrostis stolonifera*, Cent jace: *Centaurea jacea*, Dau caro: *Daucus carota*, Gal veru: *Galium verum*, Leo hisp: *Leontodon hispidus*, Mol caer: *Molinia caerulea*, Pic hier: *Picris hieracioides*, Poa ang: *Poa angustifolia*.

Abb. 5. Wahrscheinlichkeit des Vorkommens von Arten in unterschiedlichen Plot-Typen verglichen mit der Wahrscheinlichkeit des Vorkommens in allen untersuchten Plots (d. h. relative Frequenz von Arten im einzlenen Plot-Typ). Erläuterungen: helle Säulen – beweidete Einheit, dunkle Säulen – unbeweidete Einheit, Säulen mit Kreuzschraffur – Strauchinneres, Säulen mit Parallelschraffur – Strauchrand, Säulen ohne Schraffur – offene Vegetation. Sternchen bezeichnen Resultate eines Kruskal-Wallis tests für jede Art mit den Signifikanzniveaus: ***$p < 0{,}001$; **$p < 0{,}01$; *$p < 0{,}05$; $^{\#}p < 0{,}1$ (marginal signifikant). Unterschiedliche Buchstaben innerhalb einer Säulengruppe bezeichnen signifikante paarweise Unterschiede nach Mann-Whitney U-Tests ($p < 0{,}05$). Abkürzungen der Arten s. oben.

ungrazed units, the number of flowering species was significantly higher in the edge than in the shrub interiors or the open vegetation (Fig. 4B). The number of flowering species was generally higher in the ungrazed unit than in the grazed unit (Fig. 4B).

The relative flowering success of species differed significantly among plot types (Kruskal-Wallis test; $H = 13.72$, $p < 0.05$). In the grazed unit, the relative flowering success of species growing in the shrub interiors and at the edges did not differ significantly but it was significantly lower in the open pasture. In the ungrazed unit, there were no significant differences between microsite types. The relative flowering success of species was generally higher in the ungrazed unit than in the grazed one (Fig. 4C).

Out of the 15 study species, the preference indices differed significantly among microsite types in case of eight species and there were marginally significant differences in case of one species (Fig. 5). We detected that some species (*Daucus carota*, *Galium verum*, *Leontodon hispidus*, *Molinia caerulea*, *Picris hieracioides*) occurred more frequently in the shrub interiors and at the edge of shrubs than it was expected by chance, and in the case of *Daucus carota*, *Leontodon hispidus* and *Picris hieracioides* we found a clear preference for the edges. Only one species (*Agrostis stolonifera*) occurred with a higher probability in open pasture plots. The distribution of some species (*Daucus carota*, *Galium verum*, *Leontodon hispidus*, *Picris hieracioides*) was negatively affected by grazing (Fig. 5). Based on the above-mentioned species distributions, preference for microsites differed widely among species.

4. Discussion

Our results indicate that dwarf shrubs may act as biotic refuges and thus play an important role in maintaining plant diversity in pastures. Their effects on subordinate species can be different in their interior and at their edge and depends on the performance measure used (i.e. species density, flowering success). Our results are consistent with former studies that detected physical protection of palatable plants by shrubs (see CALLAWAY 2007) but we fine-tuned the description of this effect considering the different phenomenon in the interiors and at the edges of shrubs.

The similarity in species composition of plot types indicates that the detected patterns did not originate from the differences in species composition but rather from the combined effects of grazing and the occurrence of shrubs. Species densities were similar in the shrub interiors and in open vegetation both in the grazed and ungrazed units. According to several studies, biotic refuges can positively affect plant species richness by protecting plants against herbivores and ameliorating abiotic conditions (CALLAWAY et al. 2000, MILCHUNAS & NOY-MEIR 2002). These long-term effects can result in increased species richness beneath the shrubs compared with open plots where some sensitive species can disappear because of trampling and selective grazing (HAY 1986, GIBSON & BROWN 1991). However, most species that are adapted to grazing can survive in open pastures by allocating more effort to vegetative reproduction (MILCHUNAS et al. 1988). Moreover, positive effects of grazing on biodiversity were also reported because grazers can create available microsites for germination or suppress competitors (TÖLGYESI et al. 2015, TÖRÖK et al. 2016). These positive effects of grazing are typical in benign habitats with medium grazing intensity (MILCHUNAS et al. 1988). According to the model suggested by MILCHUNAS et al. (1988), it is possible that such positive effects also occurred in our study sites because they are similarly characterized by the above-mentioned conditions. Therefore the values of species density in open vegetation remained as high as those in the shrub interiors.

We did not detect any competitive effect of shrubs either in grazed or in ungrazed units; species density was similar in the shrub interiors in open plots. Besides the protection against grazing, competitive effects of biotic refuges have been reported in the literature and linked to their dense canopy and litter accumulation, which can impede light capture (BOSSUYT et al. 2005, KOYAMA et al. 2015). Therefore, the intensity of competition is generally considered to be higher below shrubs than in the open pasture. However, grazing can cause a shift in competitive interactions decreasing the intensity of above-ground competition for light and increasing the intensity of below-ground competition for soil resources (MILCHUNAS et al. 1988). Moreover, we studied the effects of small-sized deciduous shrubs, which lack permanent and intensive shading. Therefore, in pastures, competition in shrub interiors might not be necessarily higher than in open vegetation.

Species density was highest at shrub edges in the grazed and ungrazed units. Since the two neighbouring microsite types (shrub interior, open vegetation) were similar in species composition and density, this result is difficult to explain and requires further studies. A potential explanation may come from the structure of dwarf shrubs, as their peripheral surface can work as a "seed trap" (CADENASSO & PICKETT 2001, RIES et al. 2004). This can be particularly important in the case of seeds with appendices spreading primarily by wind or mammals (as they can use these shrubs for scratching) (WILLSON & CROME 1989, FAGAN et al. 1999). The endozoochory of birds can also be important, because they frequently use dwarf shrubs as perches (WILLSON & CROME 1989, VERDÚ & GARCÍA-FAYOS 2003). In line with these theoretical considerations, we detected a pronounced positive edge effect in two anemochoric (*Leontodon hispidus*, *Picris hieracioides*) species and one species characterized by both anemochory and ectozoochory (*Daucus carota*).

The flowering success (number of flowering species and relative flowering success) clearly confirmed the physical protection of understorey vegetation by thorny shrubs in the grazed units. Interestingly, the number of flowering species was highest at shrub edges in the ungrazed unit. It is likely that this result is due to the higher species richness at edges and not due to the higher average flowering success of species. After all, the relative flowering success was similar in the different microsite types. This suggests that competition in the shrub interiors was not higher than in open vegetation, where the competition by grasses can be high (AGUIAR et al. 1992, VALKÓ et al. 2012).

The protection of flowering individuals could result in an increased seed production; thus, the protected vegetation of biotic refuges can constitute local reservoires of propagules (MILCHUNAS & NOY-MEIR 2002, OESTERHELD & OYARZÁBAL 2004). This effect persisted not only below the biotic refuges but also in the edges. Livestock browse the young leaves of shrubs but the protective branch structure usually remains intact. The significantly negative effect of grazing unit on the number of flowering species indicates that grazers also grazed plants moderately below the biotic refuges, which could have resulted in a lower overall flowering success in the grazed unit (Fig. 4B–C). Outside the biotic refuges, flowering generally declined as protection was missing. Meanwhile, species densities were similar in the two types of microsites both in the grazed and the ungrazed unit. This pattern suggests that several species could have compensated their decreased reproductive success with vegetative propagation (BELSKY 1986, MILCHUNAS et al. 1988). Moreover, few individuals can produce seeds in plots in the open pasture and biotic refuges may serve as seed sources for generative colonisation (OESTERHELD & OYARZÁBAL 2004, BOUGHTON et al. 2011).

The higher flowering success in the shrub interior and at the edge of shrubs shows that biotic refuges can provide opportunity for generative propagation of plant species, promoting species long-term survival via seed rain under grazing pressure (BOUGHTON et al. 2011). According to MILCHUNAS & NOY-MEIR (2002) this mechanism is unexpectedly important in the long-term survival of grazing sensitive species in grasslands characterized by a long history of grazing. Moreover, biotic refuges can increase the resilience of pastures as they facilitate species recolonization after an intense stress or disturbance event (MILCHUNAS & NOY-MEIR 2002, FRANK 2005, BOUGHTON et al. 2011). At the landscape scale, several studies emphasize the role of habitat edges in biodiversity conservation and recommend their creation during a conscious management (HARRIS 1988, RIES et al. 2004). Our study shows edges also play an important role for maintaining biodiversity at a micro-scale, within habitats.

Our study confirms earlier recommendation for a complex grassland management regime that is characterized by high spatio-temporal diversity of management type and intensity (VADÁSZ et al. 2016). Given its flexibility, this management regime can foster a sparse native shrub population in pastures. In some types of grasslands, like in rocky grasslands or on kurgans, there are already coercive landscape elements that are tolerated by managers (MILCHUNAS & NOY-MEIR 2002, DEÁK et al. 2016a, b). In contrast, in pastures on even topography, they are removed in favour of homogeneous grassland that is dominated by herbs (FUHLENDORF & ENGLE 2001). Under such circumstances, small-sized shrubs could benefit and contribute to species conservation by acting as biotic refuges.

Erweiterte deutsche Zusammenfassung

Einleitung – Interaktionen zwischen Pflanzenarten können sich positiv oder negativ auf die betreffenden Arten auswirken. Bei der Formulierung von Managementmaßnahmen im Grasland müssen solche Interaktionen daher berücksichtigt werden. Mehrere Studien haben gezeigt, dass z. B. von Weidetieren verschmähte Pflanzenarten eine Schutzwirkung auf andere Arten haben können und dann für diese Arten biotische Refugien darstellen können (SMIT et al. 2009). Dornensträucher, die vom Vieh verschmäht werden, können z. B. vom Vieh bevorzugte Futterpflanzen vor Fraß schützen und zudem die Umweltbedingungen für diese Arten verbessern, indem sie ein ausgeglichenes Mikroklima schaffen (BOSSUYT et al. 2005). Auf diese Weise können von den Weidetieren verschmähte Pflanzenarten die Samenproduktion anderer Futterpflanzen steigern, was sich wiederum positiv auf die gesamte Artendiversität auswirken kann (CALLAWAY et al. 2000). Im unbeweideten Grasland sollten Sträucher dagegen eher eine negative Konkurrenzwirkung auf die krautigen Arten haben (SMIT et al. 2009). Neben diesen grundsätzlich bekannten biotischen Interaktionen zwischen verschmähten Sträuchern und Futterpflanzen, können Sträucher noch weitere positive Funktionen erfüllen, z. B. als Samenfallen (RIES et al. 2004). Trotz der hohen Anzahl von Studien über biotische Refugialmechanismen in Weiden gibt es nur unzureichende Kenntnis über die kleinräumigen Effekte von nicht-schmackhaften Sträuchern auf krautige Pflanzenarten im Unterwuchs. In dieser Studie untersuchen wir den Effekt von kleinen Sträuchern der Art *Crataegus monogyna* auf die krautigen Pflanzenarten im Unterwuchs und im Randbereich der Sträucher. Dazu bestimmten wir die Individuendichte und den Blüherfolg der krautigen Pflanzenarten im Strauchinneren und am Strauchrand sowie außerhalb der Sträucher.

Material und Methoden – Die Untersuchungen wurden im Juni 2015 in einer Wiesensteppe in der zentralen ungarischen Tiefebene durchgeführt. Die untersuchte Weide teilte sich in eine mit mittlerer Beweidungsintensität beweidete Fläche und eine unbeweidete Fläche. Dieser Umstand erlaubte uns die Anwendung eines Split-Plot-Designs. Unsere Studie beschränkte sich auf kleinwüchsige *Crataegus monogyna*-Sträucher mit einem Durchmesser von 30–40 cm und einer Höhe von 30–50 cm (Abb. 1). Sowohl auf der beweideten als auch auf der unbeweideten Fläche wurde die Vegetation auf 10 × 10 cm-großen Aufnahmequadraten in je drei Mikrohabitattypen untersucht. Die Mikrohabitattypen umfassten das Strauchinnere, den Strauchrand und die Offenfläche außerhalb der Sträucher (Abb. 2). Zur Untersuchung des Strauchinneren wurde ein Gitter aus 3 × 3 Aufnahmequadraten auf den Strauch projiziert. Am Strauchrand wurden zwölf Aufnahmequadrate platziert. Die Kontrolle auf der Offenfläche bestand schließlich aus 21 Aufnahmequadraten. Eine solche Aufnahmegruppe bestand wiederum aus einem Strauch und drei Kontrollgruppen. Insgesamt gab es auf der beweideten und unbeweideten Fläche jeweils acht Aufnahmegruppen. In jedem Aufnahmequadrat wurden alle Gefäßpflanzenarten und die Existenz von Reproduktionsorganen (Blüten/Früchte) notiert. Mit Hilfe einer PCA-Ordination wurde die Ähnlichkeit der Artenzusammensetzung zwischen den Mikrohabitattypen auf der Basis der relativen Frequenzen der Arten verglichen. Um den Effekt der Beweidung und der Mikrohabitattypen sowie die Interaktion zwischen Beweidung und Mikrohabitattypen auf die Artendichte und Anzahl der blühenden/fruchtenden Arten zu untersuchen, nutzten wir generalisierte lineare Modelle (GLMs) mit Poisson-Verteilung. Der relative Blüherfolg wurde mit Hilfe eines Indexes erfasst. Ein Indexwert von 1 bedeutete eine gleiche Blühwahrscheinlichkeit einer Art in einem betreffenden Mikrohabitattypen und über alle sechs Mikrohabitattypen (Nullhypothese). Ein Indexwert größer oder kleiner 1 bedeutete eine im Vergleich zum Nullmodel höhere oder niedrigere Blühwahrscheinlichkeit. Unterschiede zwischen den Mikrohabitattypen in den abhängigen Variablen wurden mit U-Test-Statistik nach Mann-Whitney auf Signifikanz untersucht (ZAR 1999).

Ergebnisse – In der PCA-Ordination überlappten sich die Konvexhüllen der Mikrohabitattypen stark; dies deutete auf keine nennenswerten Unterschiede in der Artenzusammensetzung zwischen den Mikrohabitattypen hin (Abb. 3). Allerdings war die Artendichte am Strauchrand signifikant höher als im Strauchinneren oder außerhalb der Sträucher (Abb. 4A). Die höchste Artendichte wurde am Strauchrand auf der unbeweideten Fläche gemessen. Insgesamt zeigten die Ergebnisse auf der beweideten und unbeweideten Fläche jedoch ein ähnliches Muster. In den GLMs hatten Beweidung und Mikrohabitattyp auf die Anzahl der blühenden Pflanzenarten signifikante Effekte; zudem interagierten Beweidung und Mikrohabitattyp in ihrer Wirkung signifikant. Auf der beweideten Fläche unterschied sich die Anzahl der blühenden Pflanzenarten zwischen Strauchinneren und Strauchrand nicht signifikant; sie war jedoch außerhalb der Sträucher signifikant niedriger als im Strauchinneren oder am Strauchrand. Auf der unbeweideten Fläche war die Anzahl der blühenden Arten am Strauchrand signifikant höher als im Strauchinneren und außerhalb der Sträucher. Grundsätzlich war die Anzahl der blühenden Arten auf der unbeweideten Fläche höher als auf der beweideten Fläche (Fig. 4B). Auf der beweideten Fläche unterschied sich der relative Blüherfolg nicht zwischen Strauchinnerem und Strauchrand; außerhalb des Strauchs war der Blüherfolg aber auf signifikant niedriger. Auf der unbeweideten Fläche zeigten alle drei Mikrohabitattypen einen ähnlich hohen relativen Blüherfolg (Fig. 4C).

Diskussion – Unsere Ergebnisse deuten darauf hin, dass kleine Sträucher in Weiden für krautige Arten biotische Refugien darstellen können und diese damit für den Naturschutz eine Bedeutung haben. Ausmaß und Richtung der Wirkung variierten allerdings zwischen den Mikrostandorten – im Strauchinneren, am Strauchrand und im außerhalb des Strauchs – und hängen auch von der Betrachtung der Artendichte oder des Blüherfolgs ab. Unsere Ergebnisse decken sich mit früheren Studien, die ebenfalls einen Schutzeffekt von Sträuchern auf Futterpflanzen nachweisen konnten (CALLAWAY et al. 2000). Interessanterweise fanden wir jedoch keine negativen Konkurrenzeffekte durch die Sträucher (weder auf der beweideten noch auf der unbeweideten Fläche). Überraschenderweise war die Artendichte sowohl in der beweideten als auch auf der unbeweideten Fläche am Strauchrand am höchsten. Dieses Ergebnis kann dadurch erklärt werden, dass die Randflächen der Sträucher als Samenfallen für andere Arten fungieren können (RIES et al. 2004). Die Analyse des Blüherfolgs (Anzahl der blühenden Arten, relativer Blüherfolg) zeigte dagegen, dass dornige Kleinsträucher den Unterwuchs vor Fraß schützen können. Dieser Effekt war sowohl im Strauchinneren als auch am Strauchrand zu beobachten. Der signifikant-negative Effekt der Beweidung auf die Anzahl der blühenden Arten im Strauchinneren und am Strauchrand deutete an, dass die Weidetiere die Blüten der krautigen Pflanzen zu einem gewissen Ausmaß auch unter den Sträuchern fressen (Abb. 4B). Außerhalb der Sträucher verzeichneten wir eine Abnahme des Blüherfolges, weil hier kein Schutz vor Beweidung bestand. Biotische Refugien wie kleine Dornensträucher können somit in Weiden die generative Vermehrung fraß-sensitiver Pflanzenarten ermöglichen und damit (als dauerhafte Samenquelle) das Überleben dieser Arten in den angrenzenden beweideten Flächen sichern helfen (BOUGHTON et al. 2011). Unsere Studie untermauert bestehende Forderungen nach einer differenzierten Graslandpflege mit hoher raumzeitlicher Vielfalt an Maßnahmen und deren Intensität (VADÁSZ et al. 2016). In Weiden sollte daher eine spärliche Kleinstrauchpopulation ein Bestandteil eines solchen mehrschichtigen Pflegekonzepts sein.

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