



Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee



Biodiversity in low-intensity pastures, straw meadows, and fallows of a fen area—A multitrophic comparison

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ARTICLE INFO

Article history:

Received 28 May 2015

Received in revised form 30 November 2015

Accepted 15 December 2015

Available online xxx

Keywords:

Restoration

Pastures

Meadows

Fallows

Wetland biodiversity

Conservation

Plants

Auchenorrhyncha

Araneae

ABSTRACT

Despite the Europe-wide protection of wetlands, knowledge on the performance of management strategies for biodiversity conservation across different trophic levels is still relatively scarce. Here, we compare old straw meadows with restored low-intensity pastures and with fallows in a fen area in the northern pre-Alps. We sampled biodiversity at three trophic levels including plants, leafhoppers and spiders. Plant species richness was significantly enhanced by grazing and mowing compared with fallows. In contrast, species numbers and abundances of leafhoppers and spiders were highest in pastures and lowest in meadows. Endangered plant species were relatively rare in the restored pastures, which were still nutrient rich compared with meadows. Thus, land-use history can constrain restoration success for dispersal limited plant species in the short term. Although fallow plots were poorer in terms of species richness, their leafhopper and spider assemblages were highly differentiated and comprised a number of exclusive species, some of which were endangered. Our results suggest that maximum biodiversity can best be maintained by the diversification of management types. Enhanced abundances of leafhoppers and spiders in pastures may improve prey availability for predators such as amphibians, reptiles, and birds. Low-intensity grazing is currently rather uncommon in Central European fens, but our results encourage more widespread use of cattle for managing this type of habitat.

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1. Introduction

Intense mowing and grazing can have a strong detrimental impact on grassland biodiversity at various trophic levels (Morris and Lakhani, 1979; Gibson et al., 1992; Kruess and Tschardtke, 2002), especially when combined with fertilization, drainage and reseeded (Day and Detling, 1990; Huntly, 1991; Watkinson and Ormerod, 2001). Highly productive grasslands are often characterized by low floral diversity due to the exclusion of competitively inferior plant species by dominant, fast-growing species (Hautier et al., 2009). In contrast, low-intensity grazing and mowing are generally expected to enhance plant diversity (Collins et al., 1998; Olf and Ritchie, 1998). The removal of plant biomass through

grazing or mowing reduces light competition and enables the growth of less competitive plant species (Milchunas et al., 1988; Huntly, 1991; Belsky, 1992). Compared with small mammals, cattle are particularly well-suited for grassland management because they can use low-quality food (i.e., dominant plants such as reed and sedges) and increase habitat heterogeneity by creating disturbance patches (Olf and Ritchie, 1998). In addition, trampling and faecal deposition can increase regeneration sites and soil heterogeneity (Steinauer and Collins, 1995; Schrama et al., 2013).

According to earlier theoretical work, plant diversity is considered a major determinant of the diversity at higher trophic levels (Hutchinson, 1959; Root, 1973; Hunter and Price, 1992). However, this statement is not well supported by more recent studies (Vessby et al., 2002; Castagneyrol and Jactel, 2012; van Klink et al., 2015). The effect of mowing on arthropods might differ from effects on plants: during mowing the vegetation and most of its inhabitants are removed in one catastrophic event, thus dramatically reducing shelter, food resources and deposited eggs and also causing direct mortality among arthropods (Morris, 1981;

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Nickel and Ahtziger, 1999, 2005). In contrast, low-intensity grazing poses a spatially and temporally heterogeneous disturbance that is expected to be less disruptive to animal populations. Traditional management types like mowing once a year in autumn or low-intensity grazing, are often associated with high biological

diversity, and restoration by low-intensity management measures can improve biodiversity in formerly intensively used fields (Tschamtk and Greiler, 1995; Wettstein and Schmid, 1999).

Hence, management of wet grasslands for biodiversity conservation poses a number of dilemmas for applied ecologists: too

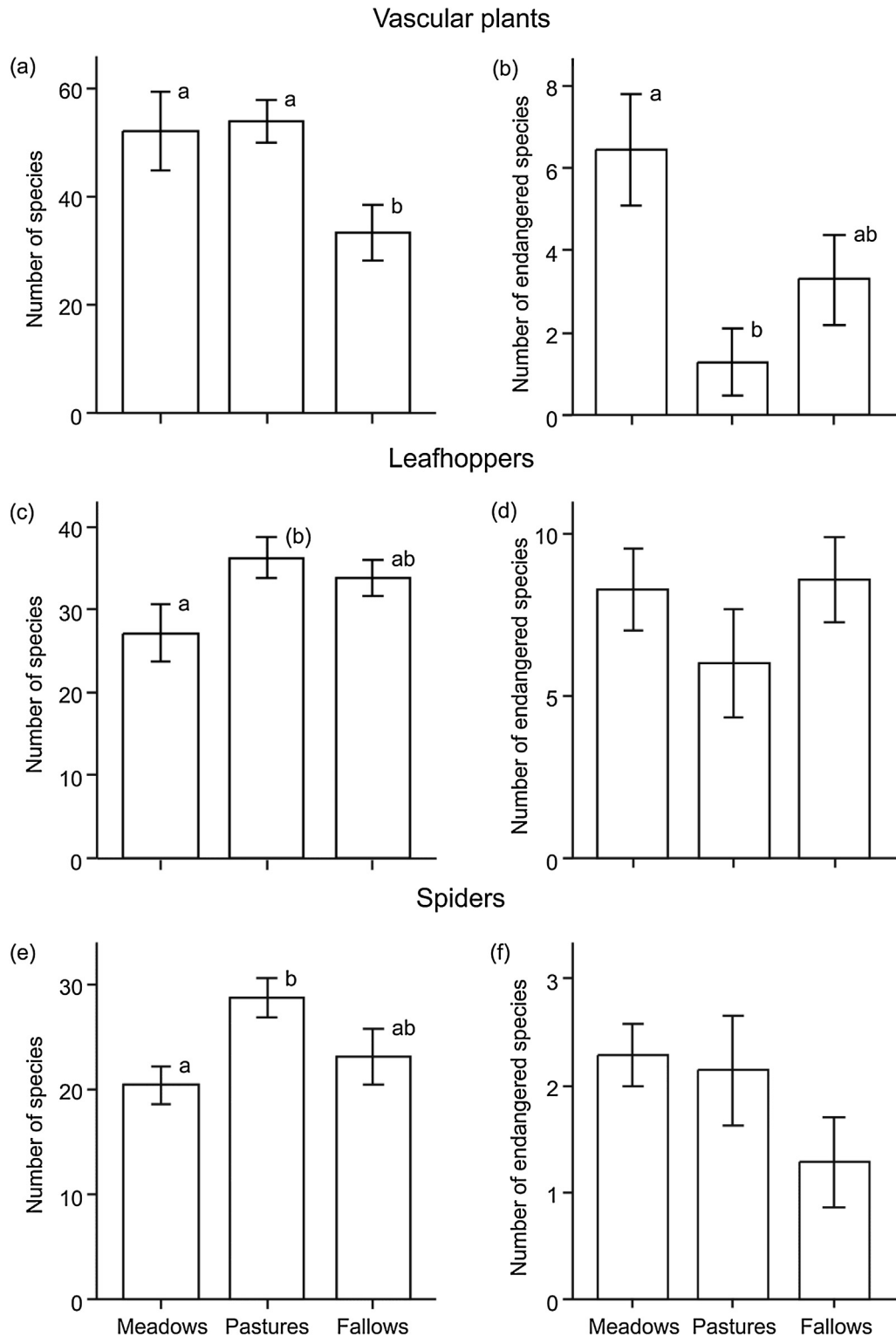


Fig. 1. Species richness of plants (a) and (b), leafhoppers (c) and (d) and spiders (e) and (f) in pastures, fallows and meadows (mean ± SE). The numbers of plant species (a) and spider species (e) were significantly affected by the management. For leafhoppers (c) we observed a statistical trend regarding management effects. The number of endangered plant species (b) differed between the three management types. No significant effects of management were found on endangered leafhoppers (d) and spiders (f). Treatments with different letters are significantly different ($p < 0.05$) between pastures, fallows and/or meadows (post-hoc comparison of means). Letters in parentheses indicate a statistical trend ($p < 0.1$).

much management may lead to land degradation and loss of biodiversity, while too little management may lead to succession from grassland to woodland and the loss of grassland habitats (Watkinson and Ormerod, 2001). In addition, management strategies optimal for plant conservation may impair the survival of arthropods, especially if uniformly applied to large areas (Cattin et al., 2003; Schmidt et al., 2008). Thus, differentiated management may be needed to meet the conservation demands of different groups of organisms. A considerable number of studies have already been published on effects of conservation managements such as grazing or mowing on plant and arthropod diversity (reviewed by Swengel, 2001; Middleton et al., 2006; van Klink et al., 2015). However, the vast majority of these studies focused on one single taxon (van Klink et al., 2015).

Here we compare effects of low-intensity cattle grazing, late-annual mowing and fallowing on highly abundant, highly diverse and functionally important groups representing three trophic levels: plants, leafhoppers (meant here as Auchenorrhyncha including also planthoppers) and spiders. We expect substantial differences in the numbers of species between the three management types. Specifically, plants are expected to benefit mainly from mowing, while species numbers and abundances of leafhoppers and spiders should be enhanced by low-intensity grazing. Due to different habitat preferences and differences in their sensibility to disturbances among species, we expected distinct communities of the respective groups between the three management types. We further expect a negative relationship between plant species richness and nutrient availability and a positive relationship between plant species richness and the number of leafhopper species, which feed on few or only one plant species.

2. Methods

2.1. Study sites

In May 2014, 21 sites were selected in a fen area of one square kilometer along a peat bog margin north of the town of Kißlegg, Germany (47°49'06"N/9°53'07"E). Seven sites were old and traditionally managed straw meadows, which are mown annually in late summer for gaining winter straw. Another seven sites were restored low-intensity pastures on formerly intensively used meadows. These pastures have been grazed for 10–15 years with cattle (approx. one livestock unit per hectare and year, during summer). The remaining seven sites were fallows mown on an irregular basis (every 3–30 years) to prevent tree encroachment. At each site we established two crosswise transects (length: 50 m) marked with wooden pegs at the starting points and the intersection.

2.2. Field methods

We sampled all groups of organisms in late May, at the beginning of July, and mid-September 2014. Plant species, vegetation height, the cover of vascular plants, and the percentage of bare ground were recorded within a 2 m wide strip along each transect. Plant taxonomy follows Breunig and Demuth (1999). Leafhoppers and spiders were collected along transects with suction sampling (25 times 5 s per transect, suction tube opening with a diameter of 14 cm) with a modified STIHL SH 85 leaf blower. The catch was transferred into a large white plastic box, and all visible leafhoppers and spiders were taken with aspirators. Leafhopper sampling was complemented by standardized sweep netting (50 beats per transect, with a D-shaped sweep net frame 32 cm broad) to include also species living in the higher vegetation strata. Pitfall traps were used to sample ground-dwelling spiders.

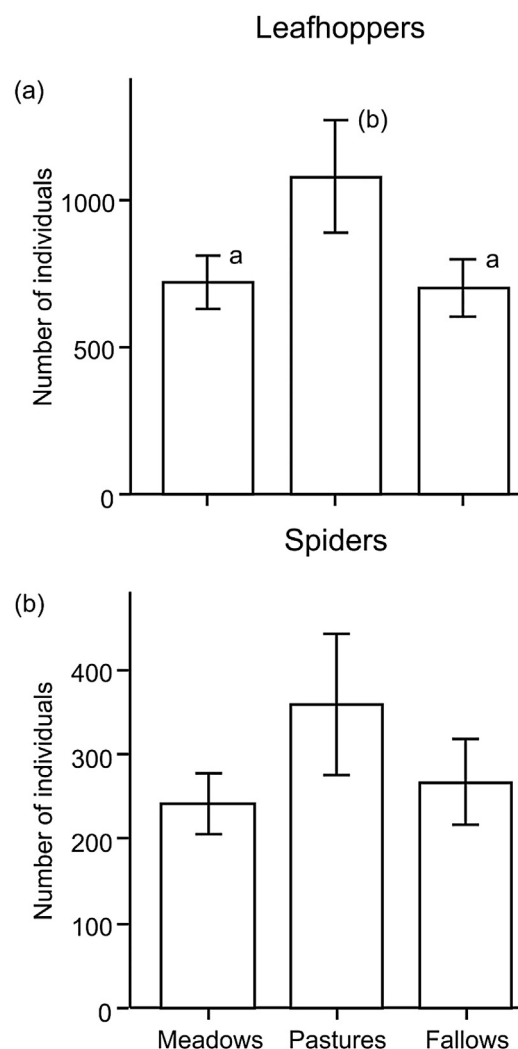


Fig. 2. Abundances of leafhoppers (a) and spiders (b) in pastures, fallows and meadows (Mean \pm SE). We observed a trend towards higher leafhopper densities in pastures compared with meadows and fallows. Spider abundance was unaffected by management. Letters next to standard error bar indicate significant differences ($p < 0.05$) or statistical trends ($p < 0.1$) if written in parentheses.

Four pitfall traps per site were distributed on the transects. As capture fluid, we used a 30% ethylene glycol solution (with some droplets of soap and 1 g Quinine chloride per litre as a bitter agent to prevent mammals from drinking the fluid; see Jud and Schmidt-Entling, 2008). The pitfall traps were installed during each suction sampling round and operated for 2 weeks. Leafhoppers and spiders were transferred to 90% ethanol and identified to species level in the laboratory. Juvenile leafhoppers were also identified to species level (from instar II/III onwards; see Stöckmann et al., 2013), juvenile spiders were identified to family. Leafhopper taxonomy follows Nickel and Remane (2002) and the taxonomy of spiders corresponds to the World Spider Catalog, version 16 (2015).

2.3. Statistical analysis

All data were pooled per site (seven sites per management type). The conservation status of plant species (only the categories 1–3) was retrieved from the red-list for the pre-Alps of the federal state Baden-Wuerttemberg (Breunig and Demuth, 1999). The conservation status of leafhoppers and spiders (categories 1–3) was retrieved from the national red lists (Blick et al., in press; Nickel et al., in press). Species richness, the number of endangered

species, and the abundances of leafhoppers and spiders were compared among the three management types using generalized linear models with quasi-poisson error distribution followed by an ANOVA (χ^2 -test for the overall effect and Tukey-test for the pairwise comparison of means). Plant, leafhopper, and spider communities were compared with non-metric multidimensional scaling (NMDS) followed by a PERMANOVA based on 1000 permutations using adonis from the R-package vegan (Oksanen et al., 2013). From the same R-package we used the betadisper function to compare the homogeneity of multivariate dispersion as an estimate of beta-diversity (Anderson et al., 2006). Differences in the mean distance to the centroid were tested with ANOVA (F-test and Tukey-test). Ellenberg indicator values for moisture and nitrogen were calculated for every site. This is a well-established and reliable method to characterize environmental variables of study sites based on plant species (Schaffers and Sýkora, 2000; Diekmann, 2003). Vegetation characteristics were compared among the three management types using ANOVA (F-test). To test for the relative importance of environmental factors in determining species richness we calculated generalized linear models following quasi-poisson error distribution. Here, the management types, moisture index, nitrogen index and plant species richness (for leafhoppers and spiders only) entered the full models as fixed effects. Model selection was based on QAICc using the dredge function from the MuMIn R-package. The final model was tested with a Type-II ANOVA (χ^2 -test). All statistical analyses were conducted in R version 3.1.2 (R Development Core Team, 2014).

3. Results

3.1. Species richness and number of endangered species

Altogether we recorded 195 plant species, 146 leafhopper species, and 113 spider species. Plant species richness was significantly enhanced by grazing (mean \pm SE: 51.86 ± 7.25) and mowing (53.86 ± 3.96) compared with fallows (33.14 ± 5.13) (Fig. 1a; $\chi^2_{2,18} = 8.53$, $p = 0.014$). Species numbers of leafhoppers tended to be higher in pastures (36.29 ± 2.39) compared with meadows (27.14 ± 3.45) (Fig. 1c; $\chi^2_{2,18} = 5.73$, $p = 0.057$). Similarly, species numbers of spiders were higher in pastures (28.71 ± 4.82) than in meadows (20.43 ± 1.80) (Fig. 1e; $\chi^2_{2,18} = 7.49$, $p = 0.024$).

We sampled 31 plant species, 34 leafhopper species, and 12 spider species that are considered as endangered based on the respective red-lists. Numbers of endangered plant species were significantly higher in meadows (6.43 ± 1.34) compared with pastures (1.29 ± 0.81) (Fig. 1b; $\chi^2_{2,18} = 9.83$, $p = 0.007$). The number of endangered leafhoppers and spiders were not significantly affected by the management type (leafhoppers: Fig. 1d; $\chi^2_{2,18} = 1.94$, $p = 0.380$, spiders: Fig. 1f; $\chi^2_{2,18} = 3.34$, $p = 0.188$).

3.2. Abundances of leafhoppers and spiders

In total, 17482 leafhopper and 6071 spider individuals (including juveniles) were collected at our sites. The abundance of leafhoppers tended to be higher in pastures (1078 ± 189) compared with fallows (701 ± 96) and meadows (719 ± 90) (Fig. 2a; $\chi^2_{2,18} = 5.45$, $p = 0.065$). The abundance of spiders was not significantly affected by the management type alone (Fig. 2b; $\chi^2_{2,18} = 2.14$, $p = 0.34$).

3.3. Differences in species assemblages

Pastures, meadows and fallows were all characterized by different and specific plant species assemblages (Fig. 3a; pseudo- $F_{2,18} = 3.15$, $p < 0.001$). The same was the case for leafhoppers

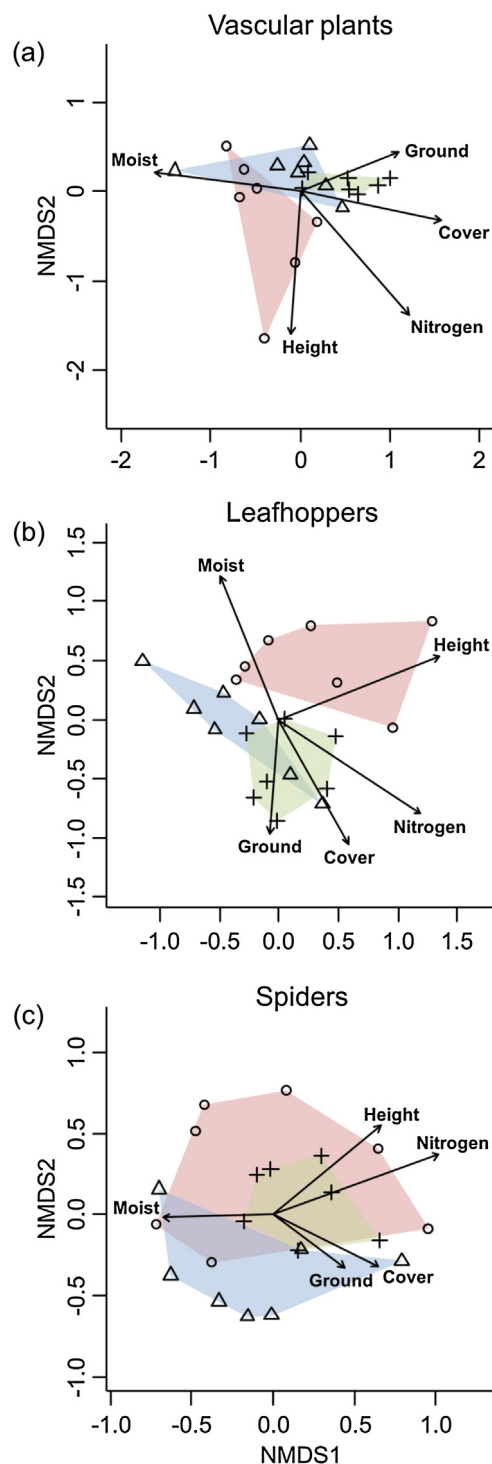


Fig. 3. Nonmetric multidimensional scaling (NMDS, based on Bray–Curtis similarity) of the plant (presence/absence), leafhopper, and spider assemblages among seven sites per land use type (Δ = meadows, $+$ = pastures, and \circ = fallows). The arrows represent characteristics of the study sites (height = vegetation height (cm), cover = vegetation cover (%), ground = bare ground (%), moist = moisture index, and nitrogen = nitrogen index; see Table 1). The polygons comprise all seven sites of the respective management type (blue = meadows, green = pastures, and red = fallows). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

(Fig. 3b; pseudo- $F_{2,18} = 1.86$, $p = 0.02$), but not for spiders (Fig. 3c; pseudo- $F_{2,18} = 1.27$, $p = 0.17$). For spiders, beta-diversity was significantly different across the management types ($F_{2,18} = 4.21$, $p = 0.032$) with higher beta-diversity in fallows compared with

meadows (contrast, $p = 0.028$). For leafhoppers and plants we could not reject homogeneity of multivariate dispersion at the 0.05 error level (leafhoppers: $F_{2,18} = 2.49$, $p = 0.11$; plants: $F_{2,18} = 1.80$, $p = 0.19$).

3.4. Factors driving biodiversity

Plant species richness was negatively correlated with the moisture index and the nitrogen index (moisture: $\chi^2_{1,19} = 13.51$, $p < 0.001$; nitrogen: $\chi^2_{1,19} = 8.45$, $p = 0.004$). The number of endangered plant species strongly declined with increasing nutrient availability ($\chi^2_{1,19} = 20.70$, $p < 0.001$). Leafhopper species richness was strongly affected by the management type ($\chi^2_{2,18} = 25.58$, $p < 0.001$) and was positively correlated with the number of plant species ($\chi^2_{1,19} = 26.39$, $p < 0.001$). The number of endangered leafhopper species increased with increasing humidity and plant species richness (moisture: $\chi^2_{1,19} = 15.39$, $p < 0.001$; plant species: $\chi^2_{1,19} = 15.33$, $p < 0.001$). The number of spider species was positively correlated with moisture, nutrient availability and plant species richness (moisture: $\chi^2_{1,19} = 4.85$, $p = 0.028$; nitrogen: $\chi^2_{1,19} = 8.50$, $p = 0.004$; plant species: $\chi^2_{1,19} = 8.08$, $p = 0.004$). None of the entered parameters could explain considerable amount of variation in the number of endangered spiders (For more detail about the validity of the final models see Table 2).

4. Discussion

4.1. Vascular plants

As expected, species richness of plants was higher in meadows and pastures compared to fallows, which is likely due to reduced competition for light connected to the regular removal of biomass (Collins et al., 1998; Hautier et al., 2009). However, richness of endangered plant species was distinctly higher in meadows compared with pastures. Our analyses confirm a strong role of nutrients in determining the conservation value of plant communities as indicated by the Ellenberg nitrogen index (Bobbink et al., 2010; Stevens et al., 2010; De Schrijver et al., 2011). Here, nutrient availability was higher in the pastures compared with meadows and fallows (see Table 1), indicating that the formerly intensively used pastures are still relatively nutrient-rich compared with old, traditionally used meadows. Notably, the higher nutrient availability on pastures did not reduce overall plant species richness, but only richness of endangered plant species. Grazing should reduce nutrient availability over time if animals do not receive additional fodder. However, ten years of low-intensity grazing may not have been sufficient for a marked reduction in nutrient availability. This is in accordance with (Pykälä, 2003), who found

Table 1

Comparison of the vegetation structure and of the Ellenberg indicator values (Mean \pm SE) among the three management types (LM, ANOVA).

Management type	Meadows	Pastures	Fallows	Statistics	
Vegetation characteristics				$F_{2,18}$	p
Vegetation height (cm)	37.1 \pm 4.1	49.9 \pm 5.9	95.6 \pm 23.4	4.74	0.022
Vegetation cover (%)	78.9 \pm 7.3	89.0 \pm 1.7	75.0 \pm 3.9	2.18	0.142
Bare ground (%)	2.1 \pm 1.0	4.1 \pm 0.8	0.7 \pm 0.4	4.68	0.023
Moisture index	7.6 \pm 0.2	6.9 \pm 0.2	7.8 \pm 0.2	6.69	0.007
Nitrogen index	3.5 \pm 0.3	4.9 \pm 0.2	4.0 \pm 0.5	4.16	0.033

higher plant diversity on old pastures compared to newly-established ones after only ten years of grazing.

In addition to nutrient residues, seed banks are often depleted in intensively used grasslands and it takes time for plants to recolonize restored wetlands (Bakker and Berendse, 1999). Thereof, rare sedge meadow species are more strongly affected than readily dispersed ruderal species (Zedler, 2000). Both, nutrient residues in the soil and dispersal limitation of plants can constrain the restoration of biodiversity in grasslands (Bakker and Berendse, 1999). Thus, it is crucial to consider the land-use history of target areas when defining conservation management strategies. Although endangered species were still rare on restored pastures compared with meadows, further studies are needed to determine whether low-intensity grazing can be beneficial for endangered plants in a longer term.

4.2. Leafhoppers

The number of leafhopper species was strongly correlated with the number of plant species. There is only weak support for strong relationships between plant diversity and the diversity at higher trophic levels (Vessby et al., 2001; Castagnerol and Jactel, 2012; van Klink et al., 2015). However, the strength of this relationship may strongly depend on the degree of specialisation between plants and other trophic guilds. Thus, leafhoppers, most of which feed on plant sap of few or only one plant species (Nickel, 2003), may form an exception, rather than the rule among arthropods. Despite the high plant diversity found in meadows, their number of leafhopper species tended to be lower than in pastures, although the pastures were still very young. This can be explained by the direct mortality of mowing and the extensive removal of leafhopper individuals, deposited eggs and food resources during mowing. Although mowing in autumn is considered to be less dramatic compared with mowing that coincides with peak summer abundance of adult leafhoppers (Morris and Lakhani, 1979), mowing led to a lower leafhopper diversity in our meadows.

In accordance with other studies conducted in European wetlands, low-intensity cattle grazing enhanced leafhopper

Table 2

Effects of management and vegetation characteristics on plants, leafhoppers and spiders. Coefficients of continuous variables remaining in the final model (characters written in bold) and the percentage of variation explained by the final model (R^2) are presented. The final model was selected based on QAICc. The chosen variables did not explain variation in the number of endangered spiders.

Full model	Management	Moisture	Nitrogen	Plant species	Final model		
					R^2	df	QAICc
Model terms	(3 levels)	Coef.	Coef.	Coef.			
Plant species		-0.539	-0.272	Not entered	0.94	3	56.7
Endangered plants			-0.728	Not entered	0.84	2	56.1
Leafhopper species	Entered			0.013	0.76	4	133.7
Endangered leafhoppers		0.595		0.022	0.64	3	104.4
Spider species		0.314	0.241	0.012	0.48	4	136.6
Endangered spiders					0.00	1	68.2

diversity (Nickel and Hildebrandt, 2003). The high floral diversity as well as the heterogeneous vegetation structure may have contributed to the high species numbers in our pastures. Hygrophilous and stenotopic leafhopper species, in particular, are known to benefit from low-intensity grazing, while the number of eurytopic species declined or did not respond (Nickel and Hildebrandt, 2003). Our multivariate analysis confirms that all three management types led to specific and clearly distinct leafhopper communities and the number of endangered leafhoppers was positively correlated with the moisture index.

In addition to effects on leafhopper diversity, the abundance of leafhoppers tended to be higher in pastures compared with fallows and meadows. This finding has implications for conservation because leafhoppers can be an important prey for predators such as spiders, amphibians, and birds (Robinson and Holmes, 1982; Nentwig, 1987; Moreby and Stoate, 2001; Hodisan et al., 2010). Thus, grazing does not only enhance leafhopper diversity but has the potential to increase prey availability for higher trophic levels (Vickery et al., 2001; Evans et al., 2006; Zahn et al., 2010).

4.3. Spiders

Spiders inhabit all vegetation layers from litter to tree canopies. Web-building spiders in particular depend on the heterogeneity of vegetation structure and the availability of web-building sites (Greenstone, 1984; Bucher and Entling, 2011). Our results confirm that low-intensity cattle grazing promote spider diversity. Effects of grazing on spiders depend critically on the stocking rate and on the animal species involved. Cattle, for example, leave more biomass uneaten compared with sheep, rabbits and deer. Thus, cattle grazing at low stocking rates is particularly suitable to support high spider diversity (Bell et al., 2001). We suggest that the positive correlation between the number of spider and plant species as well as the positive correlation between the number of spider species and nutrient availability is mainly due to the heterogeneous vegetation structure in our pastures. High structural complexity of the vegetation often provides a higher diversity of niches for arthropods (Murdoch et al., 1972; Benton et al., 2003).

Despite the excellent abilities of spiders to recolonize disturbed habitats via passive aerial dispersal ('ballooning'), mowing had a detrimental effect on spider species richness. In addition to structural simplification, reduced numbers of leafhopper species and individuals and other arthropod prey may contribute to the reduced spider abundance and diversity in meadows. Another negative factor may be the absence of dung from meadows, which attracts flies and beetles that in turn enhance prey availability for spiders and other predators (Bell et al., 2001; Dennis et al., 2015).

In contrast to plants and leafhoppers, spider communities were not significantly separated between pastures, meadows and fallows. This is largely due to the large variation among the fallows included in this study (two fallows for example were dominated by reed and were inhabited by distinct spider assemblages (see Fig. 3c)). Consequently, beta-diversity of spiders was highest among fallow plots compared to pastures and meadows. Although fallows were relatively poor in terms of plant diversity, some endangered spider and leafhopper species were confined to this habitat. In addition, fallows are known to serve as refuges to endure unfavourable conditions (e.g., overwintering or during mowing, Pffiffer and Luka, 2000; Schmidt and Tscharrntke, 2005).

5. Conclusion

Our study suggests that differentiated management is optimal for conservation of biodiversity in fen areas. In particular, different management preferences were observed for plants and

arthropods. Even after a relatively short period of grazing, leafhoppers and spiders were more diverse on pastures (formerly intensified meadows) than on old straw meadows. Plants were equally diverse in meadows and pastures but endangered plant species were largely confined to old and traditionally used meadows (single late-summer cut). However, cattle grazing at low stocking rates may promote endangered plant species in a longer term. Unfortunately, arthropods are rarely considered for grassland management concepts, which are often more targeted on plants and birds (Morris, 2000; Swengel, 2001). Arthropods constitute the main fraction of terrestrial biodiversity and are the main food for numerous birds, reptiles and amphibians. Thus, their demands should be more broadly incorporated into conservation strategies.

Our results also provide arguments for the inclusion of controlled following into conservation plans. Although their average species richness was lower compared to pastures, fallows had highly differentiated arthropod communities (high beta-diversity), including a number of endangered species that were confined to these sites. Thus, we suggest that highest biodiversity can be maintained by the diversification of management types. In particular, low-intensity grazing is currently rather uncommon in Central European wetlands, but our results encourage a more widespread use of low-intensity grazing for managing this type of habitat.

Supplementary data

Data file (.xlsx) containing the list of species, conservation status, and the abundance of individuals per site for each group. The list of plant species (Table S1) includes the estimated vegetation structure and the Ellenberg indicator values for each site.

Acknowledgements

We thank Ulrich Weiland and Sepp Bauer (Verein für Naturschutz und Landschaftspflege Kißlegg) for initiating the project and for logistic help, Robert Bauer (Pro Regio Oberschwaben) for help in site choice, Stefan Schwab (Regierungspräsidium Tübingen) for administrative support. We are grateful to Franziska Möller for help in the field, Theo Blick for checking spider identifications and two anonymous reviewers for providing helpful comments on an earlier version of the manuscript. The study was supported by the Stiftung Naturschutzfonds Baden-Württemberg.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2015.12.019>.

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