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ORIGINAL PAPER

Diversification of mowing regime increases arthropods diversity in species-poor cultural hay meadows

O. Cizek · J. Zamecnik · R. Tropek ·
P. Kocarek · M. Konvicka

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Abstract Agricultural intensification reduces the biodiversity of European farmlands. Hay meadows represent an important farmland habitat, traditionally used to produce hay. With decreased demand for hay, the continuation of hay harvest is supported by Agri-environmental schemes across European Union. Modern hay harvest techniques differ from traditional manual harvest by removing the grass instantaneously over large land areas. To minimize adverse effects on meadow invertebrates, diversifying harvest operations is time and space is often recommended, but effects of such diversification are little studied. We compared the impact of uniform hay harvests with harvests executed in patchy manners, using four arthropod groups (butterflies, ground beetles, orthopterans and spiders) at productive, species-poor meadows in the Czech Republic. Butterflies, observed along transects, avoided uniformly cut units, preferring those cut as strips or blocks. In the three remaining groups, recorded using pitfall traps, a majority of species prevailed in traps located in uncut conditions. Synchronous mowing of large areas suppresses population sizes and diminishes the diversity of common arthropods. Besides of direct mortality and depletion of such resources as nectar or shelter, it synchronises sward regrowth, threatening also species requiring short-sward patches. Uniformly executed mowing contradicts the biodiversity conservation goal of Agri-environmental schemes. Diversifying the mowing operations via temporary fallows, or sequential mowing of land units, will improve the situation for common cultural meadows.

Keywords Hay meadows · Arthropods conservation · Mowing regimes · Species diversity · Agri-environmental schemes · Agricultural landscape

Introduction

Agricultural intensification and abandonment of less productive lands has critically impoverished the biodiversity of temperate farmlands, particularly in Europe (e.g., Stoate et al. 2009; Ekroos et al. 2010). Both the EEC/EU Common Agricultural Policy and the former eastern block farmland collectivisation brought about increased use of fertilisers, pesticides, and modern machinery, as well as land consolidation, irrigation and amelioration schemes, all resulting in increased production, but causing alarming declines of species from many groups of organisms (Donald et al. 2001; Kleijn et al. 2009), including insects (Conrad et al. 2006; Fitzpatrick et al. 2007; Van Dyck et al. 2009). These losses may eventually lead to erosion of crucial ecological services, such as pollination, decomposition, and soil fertility (e.g., Ghazoul 2005; Potts et al. 2009).

O. Cizek (✉) · J. Zamecnik
Hutur NGO, J. Purkyne 1616, 500 02 Hradec Kralove,
Czech Republic
e-mail: sam_buh@yahoo.com

O. Cizek · R. Tropek · M. Konvicka
Faculty of Science, University of South Bohemia,
Branisovska 31, 370 05 Ceske Budejovice, Czech Republic

J. Zamecnik
Museum of Eastern Bohemia in Hradec Kralove,
Eliscino nabrezi 465, 500 01 Hradec Kralove, Czech Republic

R. Tropek · M. Konvicka
Institute of Entomology, Czech Academy of Sciences,
Branisovska 31, 370 05 Ceske Budejovice, Czech Republic

P. Kocarek
Faculty of Science, University of Ostrava, Chittussiho 10,
701 00 Ostrava, Czech Republic

Seminatural grasslands, traditionally used for grazing and hay making, suffered at a particularly alarming rate. The magnitude of the losses is difficult to estimate, because statistics in many countries do not distinguish seminatural grasslands from grasslands in various stages of agricultural improvement. The extent of the losses is well known, e.g., for Britain, where about 97% of seminatural grasslands were lost following World War II. (van Dijk 1991). For the Czech Republic, where this study was carried out, relevant statistics do not exist, but local and regional comparisons (e.g., Skaloš 2006) point to losses over 50%, the rest being merged into land units that are, in average, 5–10 times larger than 50 years ago due to loss of hedgerows and field embankments. Invertebrates associated with seminatural grasslands are among the most threatened invertebrates across Europe (e.g., Thomas et al. 1994; Duelli and Obrist 2003). In addition to sensitive specialists, common generalists are declining as well (e.g., Conrad et al. 2006; Gaston and Fuller 2007; Van Dyck et al. 2009).

In Europe, efforts to halt the grassland biodiversity losses rely on two complementary approaches. The first is establishing reserves managed to mimic traditional use, with specific objection to promote grassland biota (Morris 2000). The second, administered as EU agri-environmental schemes [AES] (Pellet 2009), motivates farmers for environmentally benign practices. AES represent the largest monetary transfer to the European biodiversity preservation, many authors view them as a great hope for European flora and fauna (e.g., Kleijn et al. 2001; Marshall et al. 2006) and it is believed that they will eventually represent the main conservation tool for non-reserve lands (Fox et al. 2006). Although schemes for arable land exist, pastures or hay meadows cover by far the largest proportions of thus subsidised lands across Europe (Kleijn and Sutherland 2003; Stoate et al. 2009), including the Czech Republic.

Available studies of AES conservation efficiency, despite some encouraging reports (e.g., Aviron et al. 2009; Merckx et al. 2009), admit that the biodiversity effects are “mixed” at best (Kleijn et al. 2006; Roth et al. 2008). Whereas schemes targeted for specific habitat type or location tend to be successful (Brereton et al. 2008; Wrbka et al. 2008; Merckx et al. 2009), generic prescriptions applied synchronously across large regions often fail to produce diversity benefits (e.g., Kleijn et al. 2001; Blomqvist et al. 2009), and may deplete populations of endangered species (Konvicka et al. 2008). Such schemes do not promote land use heterogeneity, which is crucial for insects (Hendrickx et al. 2007), because heterogeneous environments provide multiple vital resources (e.g., Dennis et al. 2003; Pywell et al. 2005; Geiger et al. 2009).

Mowing for hay production is an important management practice in areas where winter grazing is impossible. Despite its wide use in continental Europe, a majority of studies of mowing impacts on insect diversity were carried out in England (e.g., Southwood and van Emden 1967; Morris 1979; Purvis and Curry 1978; Morris and Lakhani 1979; Morris and Plant 1983; Morris and Rispin 1988). This is somehow surprising, both if compared with much wider geographic scope of grazing effects studies (e.g., Purvis and Curry 1981; Poyry et al. 2006; Sjodin et al. 2008; Dover et al. 2011a), and if considered that mowing has historically represented a major use of more productive grasslands. In contrast to grazing, mowing exports plant biomass more rapidly, temporarily depleting resources such as herbivore food, and causing direct animal mortality (Morris 2000; Humbert et al. 2009, 2010; Dover et al. 2010). Many species find their optima under less intensive management, or under different time harvest time, than is optimal for farmers (e.g., Morris 1981a, b; Ockinger et al. 2006; Poyry et al. 2006), and such species likely persisted via tracking of temporarily existing unmown patches on traditionally mowed lands (Konvicka et al. 2008; Baguette et al. 2011). All these concerns are rising in importance, because mowing is currently practised even in some formerly grazed reserves as alternative management (Balmer and Erhardt 2000; Morris 2000).

Based on the impacts of mowing, it is often recommended to proceed in a mosaic-like manners, creating checkerboards or strips of cut and temporarily uncut sward (Humbert et al. 2009; Schmidt et al. 2008). These prescriptions are being increasingly implemented at localities of endangered species (e.g., Johst et al. 2006; Schmidt et al. 2008). There remains, however, only weak empirical evidence advocating such practices. On the other hand, the calls for mowing diversification generate resistance from the AES funding agencies, who argue that mosaic approaches are more costly than simple edge-to-edge cuts repeated several times a year, and also impair landscape aesthetics due to existence of “weedy” patches within meadows.

Here, we assess the impacts of diversification of mowing regimes on four arthropod groups with diverse life strategies (butterflies, ground beetles, orthopterans and spiders), inhabiting alluvial hay meadows within an intensively farmed Czech Republic landscape. The study was launched during preparation of a management plan for a reserve which, contrary to the most reserves in the region, was established to protect a historical scenic landscape. As a result of intensive meadow management in the past and isolation from other natural habitats, the studied meadows are species-poor, thus representing common productive grasslands of Central Europe.

Materials and methods

Study area

Babiččino údolí National Nature Reserve (50°24′52″N, 16°3′16″E, alt. 277–350 m) encompasses a 3.5 km long section of the Úpa River valley, situated amidst the intensively-farmed landscape of Eastern Bohemia, Czech Republic. The climate is moderately warm and slightly humid. The reserve is the historical heritage site of the Ratibořice mansion, famous from the 19th century patriotic novel 'Babička' (*The Grandmother*). The valley slopes are covered by deciduous forests, whereas the bottom, with average width 250 m, contains 68 ha of improved alluvial meadows. Being situated on poor acidic soils, they were mainly grazed until the 1840s, when drainage ditches were excavated, allowing using the meadows for hay making. This system persisted until the intensification period in 1970s, when use of fertilisers increased and the meadows were improved by reseeding. In the late 1980s, in order to restore a more natural grasslands character, fertilising was diminished and the meadows were sown with local mixtures.

Since this period until 2004, all the meadows have been managed by machine mowing twice per year. Because demand for hay decreased over this period, the primary reason for mowing of the reserve is to preserve its scenic character. Despite this, the mowing is commissioned to local farming cooperative, which is using the more efficient and destructive rotary mowers, in some years all meadows were even mulched. The cutting method thus represents the highly efficient technique widely across Central Europe.

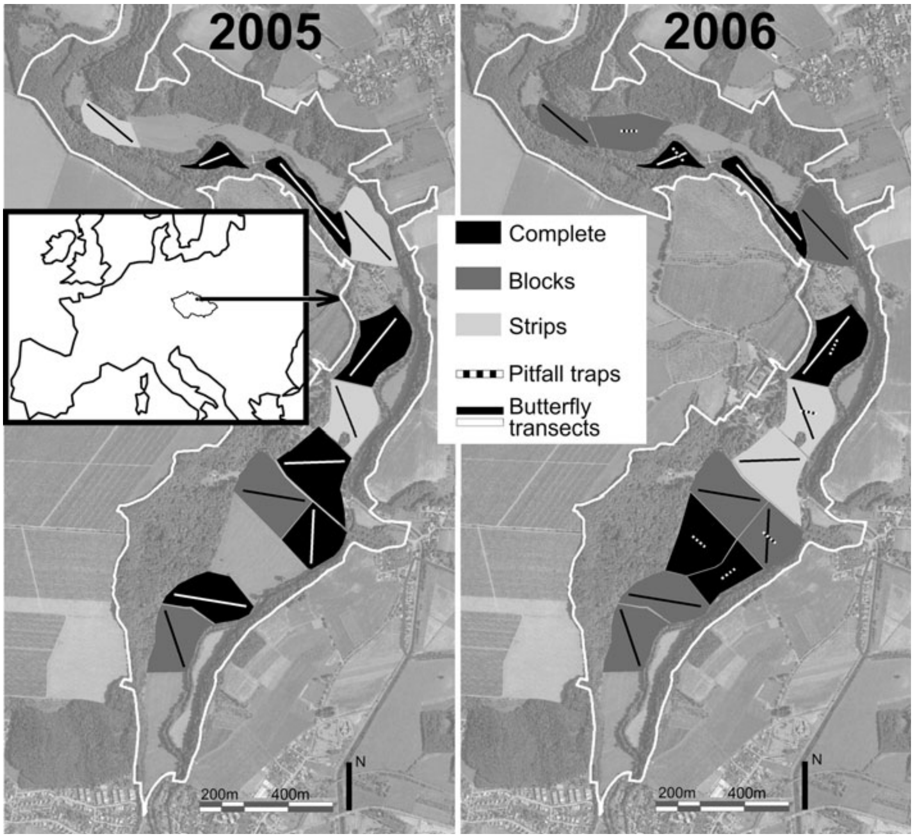
Mowing diversification experiment

Hedges, ditches, roads and the Úpa River itself divide the Babiččino údolí meadows into distinct units (Fig. 1). In 2005 and 2006, three distinct mowing regimes were experimentally applied: Complete units were mown uniformly edge-to-edge, in June and again in August; this regime is applied to a vast majority of AES meadows the Czech Republic. Strip units were mown so that during the June cut, 5–10 m wide unmown strips alternated with mown strips of a similar width, and the mown and unmown sections were switched in August. Finally, Block units were also cut only partly, but the width of unmown sections was ca 50 m.

Studied groups

We targeted four arthropod groups with diverse life histories, all often used as models in conservation studies. Butterflies are phytophagous as larvae but depend on nectar as adults, and encompass both highly mobile and sedentary species. Ground beetles are mostly ground-dwelling predators or omnivores, little dependent on the species composition of vegetation, and relatively immobile. Orthopterans are generalist phytophages or omnivores representing an important constituent of grassland insect

Fig. 1 Map of the Babiččino údolí reserve, showing the positions of differently managed hay meadow units, as applied during the study, and the positions of the butterfly transects and the pitfall-trapping sites



biomass. Spiders are predators, hunting both at the ground and in vegetation, more mobile than ground beetles.

Species names and life history information follow Benes et al. (2002) for butterflies, Kočárek et al. (2005) for orthopterans, Hůrka (1996) for ground beetles, and Buchar and Růžička (2002) for spiders.

Data collecting

Butterfly transects

We established 11 fixed linear transects (mean length 218, 21 m SE), crossing centres of 11 units (Fig. 1) but terminating 30 m from unit edges to minimise species leakage from neighbouring habitats. We walked the transects in 2005 and 2006, approximately fortnightly with 11 walks each year (from May, with the start of the first mowing, to September), always at a slow pace (ca 2 km per h) between 10.00 and 16.00 CEST and in suitable weather (>15°C, none to mild wind).

Butterflies were counted during slow walks, in a 5 m radius in front of the recorder. Transect *Length* was treated as covariable in all models. For each walk, we recorded the following *Weather* factors: ambient temperature (*Temp*), wind speed (*Wind*) and cloudiness (*Cloud*), the latter two on 1–5 ordinal scales. Covariables describing sward conditions were *Height* (averaged from 5 measurements along each transect and walk), nectar abundance (*Nabd*: ordinal 1–5 with 1 being the lowest), and nectar diversity (*Ndiv*: number of actually flowering species along the transect). The dependent variable, coded as three factors, was mowing *Regime*. Although the regime changed between the two studied years at some units (Fig. 1), the transect positions remained the same.

Pitfall traps

In 2006, we carried out pitfall trapping at seven *units* (Fig. 1), four managed by *total* cut and three as *blocks* or *strips* (herein *partial*). The traps (plastic cups: diameter 9 cm, depth 15 cm, containing 5% formaldehyde) formed lines of eight traps each, set in 8 m intervals, always in units' centres. At *partial* units, the traps were set to cut and temporally uncut parts proportionally to the representation of cut and uncut sward at the unit. The trapping, carried out from May 8 to September 17, proceeded so that the traps were always exposed for 3 days and then inactivated for 10 days. There were 10 trapping periods in total. Following each period, we sorted and identified all ground beetles, orthopterans and spiders captured.

To describe *Weather* during these 3-days trapping periods, we obtained hourly weather data from the closest meteorological station (Velichovky, 50°21′20.027″N, 15°50′31.349″E). Sums of these hourly values were used to describe wind intensity ($Wind_S$), humidity (Hum_S), solar radiation (Rad_S), precipitation ($Prec_S$) and temperature ($Temp_S$). Sward variables were *Nabd*, *Ndiv* and *Height* as for butterfly transects, but recorded within 5 m diameter circles around each trap.

Analyses

We used the redundancy analysis (RDA), a constrained linear ordination method, to relate the species composition to meadow management. We analysed separately the transect recorded butterflies and the trapped ground beetles, orthopterans and spiders, in CANOCO for Windows 4.5 (ter Braak and Smilauer 2002). Statistical significance of the ordinations was assessed via the Monte Carlo tests (999 permutations, full model). Individual transect walks and pitfall traps are herein considered as samples; species scores were divided by standard deviation, and species were centered (Lepš and Šmilauer 2003).

Butterfly transects

The explanatory variable was *Regime*, coded as a categorical variable and constant for entire unit and year. The permutation tests reflected spatial and temporal distribution of records: the two subsequent seasons were treated as blocks to filter out yearly differences; the 22 repeated walks to each transect formed whole plots, permuted as time series, whereas individual transects were permuted randomly.

Transect *Length* was treated as a nuisance covariable in all models. We tested for independent effect of *Regime*, and for its effect after filtering out *Weather* effects (an adequate weather model was obtained via CANOCO forward selection procedure from all weather covariables). In parallel, we forward-selected and tested the effects of *Sward* variables, both without and with *Weather* effects in the model. Finally, we tested if *Regime* had some residual effect on the model after *Sward* covariables, and both *Weather* and *Sward* covariables, entered the model.

Ground dwelling arthropods

The local situation around each trap and visit (i.e., if located in *cut* or *uncut* part of a unit) was explanatory variable. As *cut*, we considered sward <20 cm, which corresponds to ca. 2 weeks after mowing, and the state of individual traps changed among visits. For permutation design, entire *units* formed blocks, filtering out the effects of different locations on trap samples. The ten trapping periods were whole plots permuted as time series, and the lines of eight traps were split plots permuted as line transects.

As in case of butterflies, we first tested for the separate effect of *Regime*, and the effect of *Regime* after considering *Weather* variables. We also defined best-fitting *Sward* models, again without and with *Weather*, using CANOCO forward selection. Finally, we entered the forward-selected *Sward* variables onto the *Regime* models.

Results

Arthropod assemblage composition

The recorded assemblages were species-poor. Numbers of species/individuals were 32/2,197 for butterflies, 34/4,220 for ground beetles, 6/116 for orthopterans, and 30/8,318 for spiders. Rank-abundance plots (Fig. 2) reveal that all four assemblages were dominated by a few extremely abundant species. Over 50% of all records were represented by three butterflies (*Pieris rapae*, *Pieris napi*, *Maniola jurtina*), two ground beetles (*Poecilus cupreus*, *P. versicolor*), two orthopterans (*Chorthippus paralellus*, *Tetrix subulata*) and just a single spider (*Pardosa palustris*).

The butterfly assemblage consisted of common grasslands generalists (*Maniola jurtina*, *Coenonympha pamphilus*, *Thymelicus lineola*) and ubiquitous highly mobile species (*Pieris napi*, *P. rapae*, *P. brassicae*, *Aglais urticae*), supplemented by a high abundance of the grassland specialist *Aricia agestis*. Only two species, *Phengaris nausithous* and *P. teleius*, are endangered in the Czech Republic, but these two species were recorded in very low abundance. In the case of ground beetles, most of recorded species were widespread generalists of open habitats (*Carabus violaceus*, *Poecilus cupreus*, *Amara aenea*), supplemented by common species of more xeric (*Amara equestris*) and wet (*Agonum sexpunctatum*, *Clivina collaris*) grasslands, and a few individuals of woodland species (*Carabus coriaceus*, *Cychrus caraboides*). The most common orthopterans were two species of herbivorous *Chorthippus* grasshoppers (*C. parallelus*, *C. biguttulus*), and detritovorous *Tetrix subulata*. All spiders were also widely distributed species of open habitats (*Xysticus kochi*, *Pardosa palustris*, *Pachygnatha degeeri*), some of them displaying an affinity to wet conditions (*Pardosa amentata*, *Antistea elegans*, *Pirata latitans*).

Mowing and butterfly activity

Mowing regime had a significant effect on butterflies (Table 1). Temperature was the only significant *Weather* covariable. Filtering out the temperature effect produced an ordination, in which a majority of species avoided *Complete* cut (Fig. 3). The three species with some affinity towards *Complete* (*Araschnia levana*, *Argynnis paphia*, *Celastrina argiolus*) were woodland butterflies, probably not developing at the meadows and visiting them only temporarily. No straightforward differences in life history traits between species with affinity towards *Blocs* and *Strips* were apparent, as both regimes attracted both widespread and mobile generalists (blocks: *Aglais urticae*, *Issoria lathonia*, *Pieris rapae*; strips: *Colias hyale*, *Inachis io*, *Pieris napis*), and relatively sensitive specialists (blocks: *Aricia agestis*, *Phengaris nausithous*; strips: *Boloria dia*, *Phengaris teleius*).

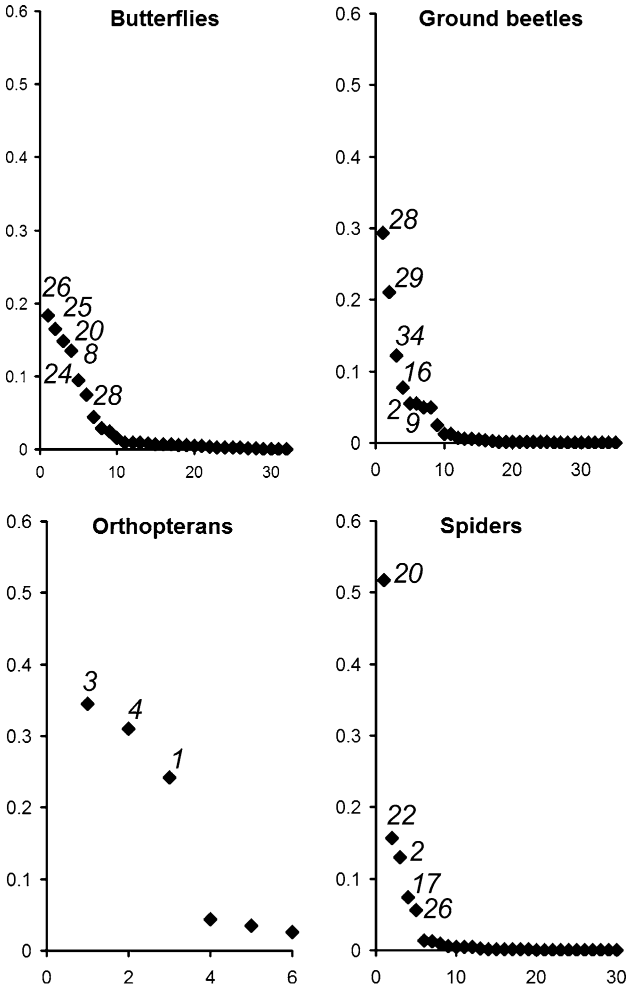


Fig. 2 Rank-abundance plots for the four arthropod groups studied for the impacts of different hay mowing regimes; *x* axis—species rank, *y* axis—abundance. Refer to Figs. 3, 4, 5, 6 for key to species numbers

Nectar supply, expressed as either *Nabd* or *Ndiv*, represented the only sward factors structuring the butterfly records (Table 1). All butterflies inclined towards high nectar supply (figure not shown). Regime model with *Nabd* as a covariate remained significant, however, suggesting some influence of other factors than nectar. A likely candidate was *Height*, because model with both *Height* and *Nabd* consumed the entire explicable variation.

Table 1 Results of the redundancy analyses (RDA) of the impact of hay harvest regime on hay meadow butterfly assemblage

	Weather	Sward	Eig.1	Eig.2	Eig.3	Eig.4	Axis 1 *F*, P^{c}	All axes *F*, P^{c}
Regime			0.010	0.002	0.357	0.140	2.52**	1.46**
Regime	*Temp*		0.010	0.001	0.315	0.140	2.82**	1.61**
Sward^{a}			0.051	0.319	0.139	0.078	14.29**	
Sward^{b}	*Temp*		0.048	0.282	0.138	0.073	14.07**	
Regime	*Temp*	*Nabd*	0.006	0.001	0.282	0.134	1.82*	1.13^{NS}
Regime	*Temp*	*Nabd +Ndiv +Height*	0.005	0.002	0.271	0.129	1.39^{NS}	1.01^{NS}

All models are after inclusion of the covariable transect length to the model. See Materials and methods for descriptions of individual predictors

Eig.1–Eig.4: Eigenvalues of the RDA ordination axes

Predictors that entered the *Sward* models: ^{a} ~*Ndiv*; ^{b} ~*Nabd*

^{c} *F* values and significances of the first and all canonical axes assessed via Monte-Carlo permutation (999 runs per analysis): ^{NS} $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

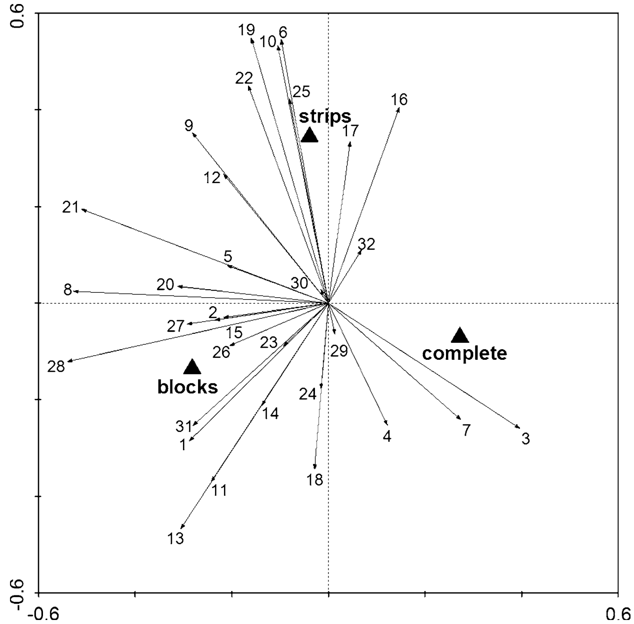


Fig. 3 Ordination diagram (RDA) showing association of butterflies with the three hay mowing regimes. 1, *Aglais urticae*; 2, *Aphanthopus hyperanthus*; 3, *Araschnia levana*; 4, *Argynnis paphia*; 5, *Aricia agestis*; 6, *Boloria dia*; 7, *Celastrina argiolus*; 8, *Coenonymha pamphilus*; 9, *Colias hyale*; 10, *Erynnis tages*; 11, *Gonepteryx rhamni*; 12, *Inachis io*; 13, *Issoria lathonia*; 14, *Lasiommata megera*; 15, *Leptidea reali*; 16, *Lycaena phlaeas*; 17, *Lycaena tityrus*; 18, *Phengaris nausithous*; 19, *Phengaris teleius*; 20, *Maniola jurtina*; 21, *Melanargia galathea*; 22, *Ochlodes sylvanus*; 23, *Papilio machaon*; 24, *Pieris brassicae*; 25, *Pieris napi*; 26, *Pieris rapae*; 27, *Polygonia c-album*; 28, *Polyomatus icarus*; 29, *Pontia daplidice*; 30, *Thymelicus lineola*; 31, *Vanessa atalanta*; 32, *Vanessa cardui*

Mowing and ground dwelling arthropods

For all three groups, *Regime* affected the composition of pitfall trap samples, even after considering *Weather* effects (Table 2). The majority of ground beetles (Fig. 4) inclined towards *Uncut* conditions. The few species inclining towards *Cut* conditions were mostly species tolerating frequently disturbed, even ploughed, environments (e.g., *Amara aenea*, *Calathus fuscipes*, *Poecilus cupreus*), whereas more specialised but still common species (such as xerophilous *Amara equestris*, hygrophilous *Epaphius secalis*, or edge specialist *Carabus coriaceus*) inclined towards *Cut* conditions. In orthopterans (Fig. 5), the polarity between *Cut* and *Uncut* conditions reflected a gradient of humidity requirements in the three most abundant species: the relatively hygrophilous *Tetrix subulata* inclined towards unmown section, generalist *Chorthippus parallelus* was intermediate, and *C. biguttulus*, a species preferring drier grasslands, inclined towards mown ones. Finally, spiders (Fig. 6) with affinity to *Uncut* conditions were mostly widespread generalists (e.g., *Erigone dentipalpis*, *Pardosa lugubris*, *Pardosa palustris*), whereas hygrophilous species (e.g., *Antistea elegans*, *Centromerus sylvaticus*, *Pardosa amentata*) inclined towards *Cut* conditions.

Testing for *Sward* conditions revealed significant effects on ground beetles and spiders. Ground beetles differed from spiders, however, so that after inclusion of *Sward* variables, *Regime* retained some significant effect on the former but not on the latter. The effects of mowing on spiders thus can be attributed solely to vegetation height and diversity, which is not the case for ground beetles. This analysis was not carried out for orthopterans, because the low total number of species did not leave any unexplained variation (Table 2).

Discussion

Hay harvest restructures arthropod assemblages in intensively managed alluvial meadows, and diversifying of mowing operations promotes biodiversity at these species-poor habitats. Transect recording of butterflies revealed

Table 2 Results of the redundancy analyses (RDA) of the impact of hay harvest regime on the assemblages of ground beatles, spiders and orthopterans

	Weather	Sward	Eig.1	Eig.2	Eig.3	Eig.4	Axis 1—F, P[e]
Ground beetle							
Regime			0.011	0.309	0.144	0.102	8.23***
Regime	$Rad_S + Wind_S + Hum_S + Prec_S + Temp_S$		0.008	0.205	0.108	0.100	6.84***
Sward[a]			0.027	0.005	0.291	0.146	19.63***
Sward[b]	$Rad_S + Wind_S + Hum_S + Prec_S + Temp_S$		0.009	0.003	0.001	0.206	7.84***
Regime	$Rad_S + Wind_S + Hum_S + Prec_S + Temp_S$	*Ndiv +Height*	0.003	0.204	0.107	0.100	3.00*
Regime	$Rad_S + Wind_S + Hum_S + Prec_S + Temp_S$	*Nabd +Ndiv +Height*	0.003	0.204	0.107	0.100	3.00*
Spiders							
Regime			0.031	0.501	0.204	0.054	21.04***
Regime	$Wind_S + Hum_S + Temp_S$		0.021	0.438	0.084	0.047	17.73**
Sward[c]			0.070	0.022	0.436	0.209	49.54***
Sward[d]	$Wind_S + Hum_S + Temp_S$		0.047	0.411	0.085	0.047	41.86***
Regime	$Wind_S + Hum_S + Temp_S$	*Nabd*	0.004	0.409	0.084	0.047	3.47^{NS}
Regime	$Wind_S + Hum_S + Temp_S$	*Nabd +Ndiv +Height*	0.002	0.406	0.083	0.047	1.89^{NS}
Orthopterans							
Regime			0.004	0.314	0.291	0.229	2.84*
Regime	$Rad_S + Wind_S + Prec_S + Temp_S$		0.007	0.298	0.282	0.202	4.63**
Sward	n.a.						
Sward	n.a.						
Regime	n.a.						
Regime	$Rad_S + Wind_S + Prec_S + Temp_S$	*Nabd +Ndiv +Height*	0.006	0.297	0.281	0.201	4.02**

Eig.1–Eig.4: Eigenvalues of the RDA ordination axes

Predictors selected for the *Sward* models for ground beetles: [a] ~*Ndiv +Height*; [b] ~*Nabd +Ndiv +Height*

Predictors selected for the *Sward* models for spiders: [c] ~*Nabd +Height*; [d] ~*Nabd*

No predictors entered the *Sward* models for orthopterans (see 'Materials and methods' for details)

[e] F values and significances of the first canonical axis assessed via Monte-Carlo permutation (999 runs per analysis): $^{NS} > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

that the overwhelming majority of species preferred units mown heterogeneously, with parts left temporarily unmown. In ground beetles, orthopterans and spiders, pitfall traps surrounded by recently cut sward differed in species composition from those surrounded by uncut sward. The effects of mowing methods were visible on a scale of hectares for butterflies, and on a scale of metres for ground beetles, orthopterans and spiders.

At the small scale of the study relative to the mobility of the invertebrates, our approach tracked invertebrate activity, rather than habitat preferences. We do not view it as a major problem. Animal activity reflects the location and distribution of their resources. From this viewpoint, mowing has two likely effects. It directly kills some individuals, and depletes resources for others, forcing them to disperse. These effects both change the composition of local assemblages (directly assessed by our sampling methods) and influence individual survival and population persistence (a main focus of conservation management).

Comparison among taxa

An overwhelming majority of butterflies inclined towards heterogeneously managed units. The impact of mowing on butterflies is easily understood, but surprisingly little appreciated. It causes direct mortality, because mowing is normally performed in early mornings, when the butterflies are still inactive (Dover et al. 2010). It also depletes nectar, forcing surviving individuals to leave or to face starvation, and destroys shelters, exposing them to adverse weather or predators. If performed over large land units, or, due to synchronisation of operations, over entire landscapes (Konvicka et al. 2008), dispersing individuals may perish before they locate new resources (cf. Dover and Settele 2009).

The analyses for butterflies reflected whole-season management, not momentary sward conditions. The results allow concluding that butterflies avoided units cut twice per year, despite the periods between cuts being sufficiently

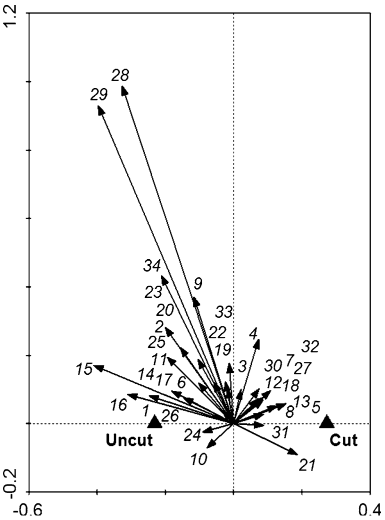


Fig. 4 Ordination diagrams (RDA) showing affinities of ground beetles to cut and uncut parts of the studied units. 1, *Agonum sexpunctatum*; 2, *Amara aenea*; 3, *Amara aulica*; 4, *Amara equestris*; 5, *Amara montivaga*; 6, *Anchomenus dorsalis*; 7, *Anisodactylus signatus*; 8, *Badister sodalis*; 9, *Bembidion properans*; 10, *Bembidion quadrimaculatum*; 11, *Calathus fuscipes*; 12, *Calathus melanocephalus*; 13, *Carabus coriaceus*; 14, *Carabus granulatus*; 15, *Carabus scheidleri*; 16, *Carabus ulrichi*; 17, *Carabus violaceus*; 18, *Cicindela campestris*; 19, *Clivina collaris*; 20, *Cychrus scarabeoides*; 21, *Epaphius secalis*; 22, *Harpalus luteicornis*; 23, *Loricera pilicornis*; 24, *Ophonus nitidulus*; 25, *Ophonus schaubergerianus*; 26, *Panagaeus cruxmajor*; 27, *Platynus assimilis*; 28, *Poecilus cupreus*; 29, *Poecilus versicolor*; 30, *Pseudoophonus rufipes*; 31, *Pterostichus nigrita*; 32, *Pterostichus ovoideus*; 33, *Pterostichus vernalis*; 34, *Pterostichus vulgaris*

long for plants to sprout new flowers. It is presumable that besides of nectar depletion, too frequent mowing affects the suitability of grasslands for butterflies in more subtle ways, such as by enhancing larval mortality. Clearly, less intensive and/or more diversified mowing will support more butterflies.

In the remaining three taxa, we worked on too small a scale to discuss landscape-level effects. Part of the patterns detected could be attributed to direct mortality caused by mechanised mowing, as in butterflies (e.g., Gardiner and Hill 2006). Still, the response variable reflected momentary sward height, and it is more legitimate to interpret the results in terms of species' behaviour.

With activity largely restricted to soil surfaces, ground beetles unlikely suffer too much mortality from mowing. Instead, they require various sheltering structures, often located in plant litter (Batary et al. 2007; Kagawa and Maeto 2009), which is more abundant in less frequently mown sward. Consequently, more species, including the most abundant ones, headed towards traps located in uncut sward. In contrast, the few species preferring drier conditions (e.g., *Amara equestris*) inclined towards shortly cut patches.

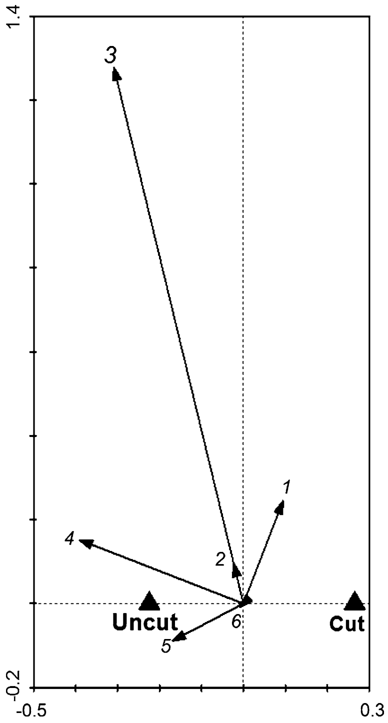


Fig. 5 Ordination diagrams (RDA) showing affinities of orthopterans to cut and uncut parts of the studied units. 1, *Chorthippus biguttulus*; 2, *Chorthippus dorsatus*; 3, *Chorthippus paralleulus*; 4, *Tetrix subulata*; 5, *Tetrix tenuicornis*; 6, *Tetrix undulata*

Unlike ground beetles and similarly to butterflies, orthopterans utilise grassland environments in a three-dimensional manner. Short homogeneous sward may be unsuitable due to the lack of tussocks that provide shelter from weather (Gardiner and Hill 2004; Gardiner and Hassall 2009) and predation.

The background of spiders' responses is likely intermediate between butterflies and ground beetles. As predators, spiders do not use nectar, but unlike ground beetles, they utilise entire three-dimensional structure of grassland environments for prey hunting, sheltering, and other activities. Indirect effects are also possible, as spiders follow the abundance of their insect prey. It was repeatedly shown that highly structured vegetation increases the diversity of spiders, the type of mowing machine plays also an important role (e.g., Bell et al. 2001; Schmidt and Tscharntke 2005).

Homogeneous versus heterogeneous mowing

Although mowing always increases the mortality and depletes resources for grassland invertebrates, the very existence of the hay meadow habitat depends on it. As illustrated by our results, mowing mode and intensity crucially affect the composition of local invertebrate assemblages. In the past, with less efficient mechanisation

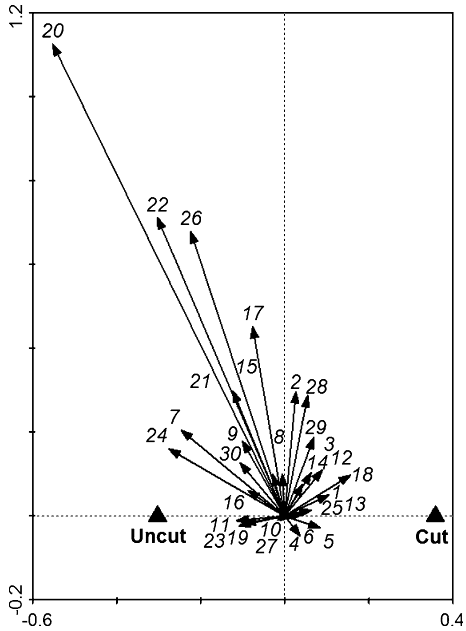


Fig. 6 Ordination diagrams (RDA) showing affinities of spiders to cut and uncut parts of the studied units. 1, *Alopecosa cuneata;* 2, *Alopecosa pulverulenta;* 3, *Antistea elegans;* 4, *Bathyphantes gracilis;* 5, *Centromerus sylvaticus;* 6, *Diplostyla concolor;* 7, *Drassyllus lutetianus;* 8, *Drassyllus praeficus;* 9, *Drassyllus pusillus;* 10, *Erigone atra;* 11, *Erigone dentipalpis;* 12, *Hahnia nava;* 13, *Hahnia pusilla;* 14, *Micaria pulicaria;* 15, *Micrargus subaequalis;* 16, *Ozyptila trux;* 17, *Pachygnatha degeeri;* 18, *Pardosa amentata;* 19, *Pardosa lugubris;* 20, *Pardosa palustris;* 21, *Pardosa prativaga;* 22, *Pardosa pullata;* 23, *Pelecopsis radicicola;* 24, *Pirata latitans;* 25, *Pisaura mirabilis;* 26, *Trochosa ruricola;* 27, *Xysticus audax;* 28, *Xysticus cristatus;* 29, *Xysticus kochi;* 30, *Zora spinimana*

and more scattered land holding, mowing proceeded patchily, reflecting the needs of individual farmers. The slow pace of manual mowing allowed the invertebrates to escape, and as it took days and weeks to mow larger units, the temporarily depleted resources had enough time to recover (Morris 2000; Humbert et al. 2009). With rapid and synchronous machinery mowing, the associated mortality likely exceeds the replacement ability of local invertebrate populations (Gardiner and Hill 2006; Schmidt et al. 2008; Dover et al. 2010). The mowing technique used also plays also a role. Although both are destructive to invertebrates, bar mowers are safer than more widely used rotary mowers (Humbert et al. 2010). Totally devastating must be mulching, which shreds biomass to small pieces.

Traditional heterogeneous mowing had yet another, rarely appreciated effect. The preference of some ground beetles, spiders and orthopterans for freshly cut surfaces indicates that short-sward patches also constitute a resource for some animal activities (e.g., butterflies bask on cut patches in cool weather: Ouin et al. 2004). Frequently mown patches certainly existed in traditional landscapes, owing to such farmers' needs as supply of green fodder during summer, and species requiring such patches likely tracked them in a similar manner as species requiring taller vegetation tracked temporarily unmown swards. Because synchronous mowing synchronises the subsequent regrowth, species requiring short sward may be impaired as seriously, as the rapid removal of biomass by modern machinery impairs tall-sward species (Berga and Gustafsonb 2007; Šálek and Schröpfer 2008).

We documented that the diversification of mowing diversifies invertebrate assemblages on very small scales (among meadows units for butterflies, and within the units for ground beetles, spiders and orthopterans), on meadows that were initially species poor. Therefore, any diversification of mowing operations will contribute to the diversity of animal resources, and hence species diversity. The finding that even common species inhabiting biologically poor grasslands responded to management diversification is important for managing grasslands with no special biological richness. Earlier studies documented that more diversified management is indispensable for sensitive grassland specialists (Johst et al. 2006; Spitzer et al. 2009). We now showed that it would also benefit common and widespread species.

Conclusion

Traditional agricultural landscapes were much more diverse, in terms of both land holding and land use, than modern intensified farmland. Everything else being equal, decreasing size of management units, increasing temporal asynchronicity of operations, or use of more diverse technologies, all benefit farmland biodiversity (e.g., Rundlof et al. 2008; Butler et al. 2009). Sadly, the homogenisation trends typical for productive farming continue even on lands subsidised for environmental goods, because funding agencies favour simple prescriptions enforceable over entire regions (Beckmann et al. 2009). This is no longer tolerable, if the massive monetary transfers of AES are to meet their goals (Dover et al. 2011b).

Even with modern technology, hay harvest can be easily diversified either in space (temporarily uncut strips or blocks) or time (sequential mowing within an area). Despite being increasingly used in grassland reserves (e.g., Morris 2000; WallisDeVries et al. 2002), these practices do not even bear an established name and are variously labelled as "rotational fallows" (Schmidt et al. 2008) or "mosaic mowing" (Konvicka et al. 2008). It is clear that insular reserves, no matter how well managed, cannot maintain regional species pools indefinitely, due to the effects of stochastic catastrophes on isolated populations (Hanski 1999; Rosenzweig 2003). Management diversification needs to expand beyond reserves, to lands farmed under environmental subsidies. The diversification measures applied in this study will unlikely restore the entire biotic richness of historical grasslands, but will certainly slow down the biodiversity loss.

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