Agriculture, Ecosystems and Environment 196 (2014) 24–33

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

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

Effects of timing and frequency of mowing on the threatened scarce large blue butterfly – A fine-scale experiment

Ádám Kőrösi [a,b,*], István Szentirmai [c], Péter Batáry [d], Szilvia Kövér [e], Noémi Örvössy [f], László Peregovits [g]

[a] MTA–ELTE–MTM Ecology Research Group, Pázmány Péter s. 1/C, Budapest 1117, Hungary
[b] Field Station Fabrikschleichach, Biocenter, University of Würzburg, Glasshüttenstr. 5, Rauhenebrach 96181, Germany
[c] Őrség National Park Directorate, Siskaszer 26/A, Őriszentpéter 9941, Hungary
[d] Agroecology, Georg-August University, Grisebachstr. 6, Göttingen 37077, Germany
[e] Institute of Biology, Szent István University, Rottenbiller u. 50, Budapest 1077, Hungary
[f] Institute of Ecology and Botany, MTA Centre for Ecological Research, Alkotmány u. 2-4, Vácrátót 2163, Hungary
[g] Pars Limited, Rózsa u. 17, Nagykovácsi 2094 Hungary

ARTICLE INFO

Article history:
Received 5 December 2013
Received in revised form 18 June 2014
Accepted 23 June 2014
Available online xxx

Keywords:
Abandonment
Central Europe
Grasslands
Habitat management
Traditional land-use

ABSTRACT

As part of a major transformation of the EU agriculture in the last few decades, traditional land-use types disappeared due to either intensification or abandonment. Grasslands are highly affected in this process and are consequently among the most threatened semi-natural habitats in Europe. However, experimental evidence is scarce on the effects of management types on biodiversity. Moreover, management types need to be feasible within the recently changed socio-economic circumstances in Hungary. We investigated the effects of timing and frequency of mowing on the abundance of the scarce large blue butterfly (*Phengaris teleius*), on the abundance of its host plant and on the frequency of its host ant species. In each of four study meadows, we applied four types of management: one cut per year in May, one cut per year in September, two cuts per year (May and September) and cessation of management. After three years of experimental management, we found that adult butterflies preferred plots cut once in September over plots cut twice per year and abandoned ones, while plots cut once in May were also preferred over abandoned plots. Relative host plant abundance remarkably increased in plots cut once in September. Management did not affect the occupancy pattern of *Myrmica* host ants. Invasive goldenrod was successfully retained by two cuts per year. To our knowledge, this is the first attempt to test management effects on the whole community module of a socially parasitic butterfly, its host plant and host ants. Based on the results, we provide recommendations on regional management of the scarce large blue's habitats.

1. Introduction

Due to changes in European agriculture following the second World War traditional land-use practices have been disappearing. Intensification in more productive regions and concurrent abandonment in less accessible and populated ones remain the major threat in reducing biological diversity in agricultural landscapes (Stoate et al., 2009). Grasslands of high biodiversity are particularly threatened by abandonment, since these habitats have been maintained for centuries by traditional, small-scale land-use practices (Cremene et al., 2005; Plieninger et al., 2006). In most cases, socio-economic factors such as rural depopulation and changes in farm size distribution cause a decline in livestock implying the decrease of grazing and hay cutting intensity (Schmitz et al., 2003; Rescia et al., 2008). Land abandonment may have multi-level and complex consequences for biodiversity and functioning of grassland ecosystems. It may cause loss, degradation and consequent fragmentation of habitats leading to the decline of biological diversity (e.g., Schmitt and Rákosy, 2007; Rösch et al., 2013). However, management cessation in grasslands may also temporarily increase species richness and abundance of butterflies (Skórka et al., 2007) and cessation of management in agricultural landscapes may even create suitable habitat for insects (Skórka and Lenda, 2010). Butterflies are especially concerned by grassland abandonment (for review see Dover et al., 2011b; Van Swaay, 2013). For example, Nilsson et al. (2008) revealed that 44% of butterflies and Burnet moths became regionally extinct in

* Corresponding author: Tel.: +36 30 392 2660.

http://dx.doi.org/10.1016/j.agee.2014.06.019
0167-8809/

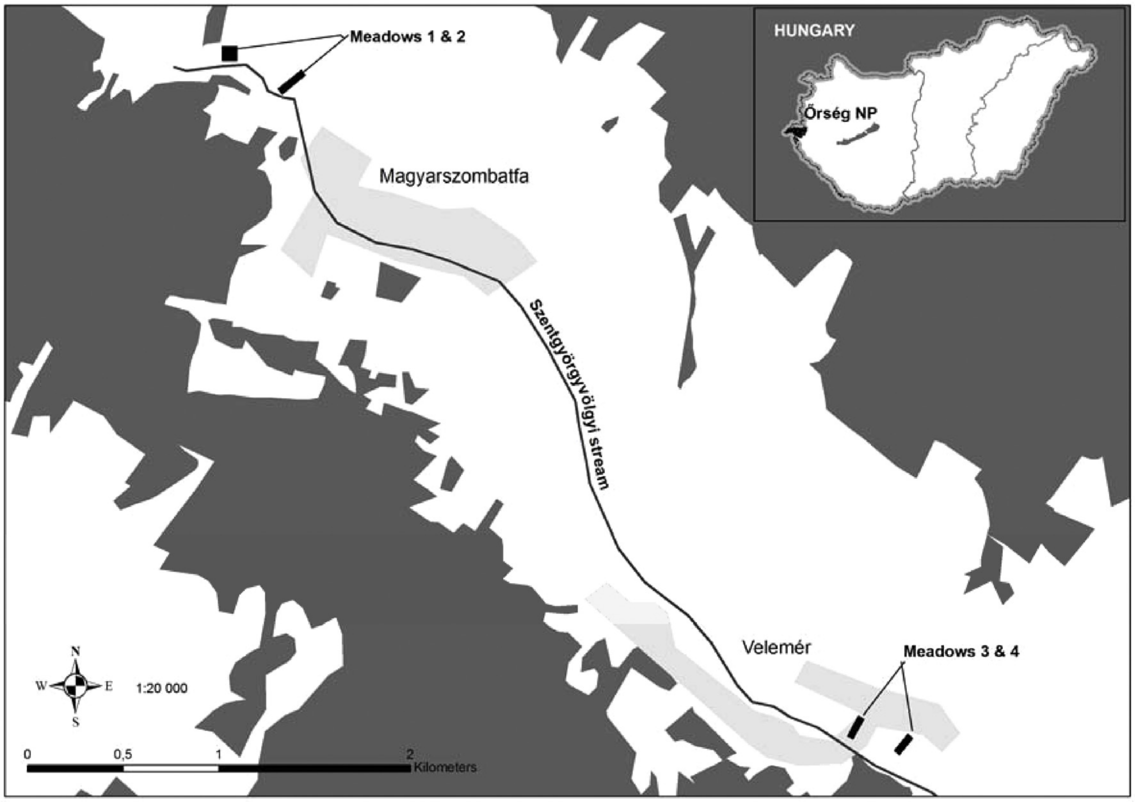

Fig. 1. Map of study sites. White: grassland; light gray: built-in area; dark gray: woodland.

Sweden during the last 190 years, and the decline coincided with the loss of flower-rich open habitats that had been maintained by late cutting. In northern Spain, Stefanescu et al. (2009) found rapid changes in the composition of butterfly communities immediately after grassland abandonment as grassland specialist species were substituted with widespread, ubiquitous butterflies, less important for conservation.

Similarly to other parts of Europe, land abandonment is caused by socio-economic factors in our study region (Őrség, Western Hungary). Agriculture has been dominated by animal husbandry, a few hundreds of cattle were fed at households in each village for centuries until the 1990s. Aging and emigration of rural population together with the market collapse of dairy products resulted in a dramatic decline (approx. 95% in the study area) in cattle numbers (Báldi and Batáry, 2011; see also Stenseke, 2006; Rescia et al., 2008 for examples from other parts of Europe). Nevertheless, current legislation of Hungary prescribes cutting grasslands once a year before 15th August. Thus hay meadows, which had been cut twice per year (in May and in September) traditionally, have been either completely abandoned or cut haphazardly, very often in the flight period of threatened butterflies. The latter has obvious detrimental effects on butterflies, while abandonment facilitates the spread of invasive weeds such as goldenrod (*S. gigantea* Aiton) (de Groot et al., 2007; Skórka et al., 2007). However, meadows in the study region are still inhabited by rich butterfly assemblages (Ábrahám, 2012). As Kleijn et al. (2009) pointed out "conservation initiatives are most (cost-) effective if they are preferentially implemented in extensively farmed areas that still support high levels of biodiversity". Therefore, we aimed to find how traditional grassland management practices could be revived in the Őrség region for the preservation of its diverse butterfly fauna.

Large blue butterflies (*Phengaris* spp., in many former publications referred as *Maculinea*) are flagship species of the European nature conservation (e.g., Settele and Kühn, 2009). Their obligate ant-parasitic life-cycle attracted much scientific interest including their functional relationships with host plants and ants, habitat-use and conservation (Settele et al., 2005). Moreover, they proved to be suitable indicator and umbrella species in hay meadows that are of particular conservation concern in Europe (Skórka et al., 2007; Spitzer et al., 2009). Due to their complicated life history and links with other organisms, the response of these butterflies to different management scenarios may possibly predict response of entire grassland ecosystem to management or (grass) land use changes, and both cessation of management and intensification may affect them considerably. However, there is a lack of evidence on how habitats of large blue butterflies should be maintained (Thomas et al., 2011). In their review, Van Swaay et al. (2012) provided some guidelines for the habitat management of *Phengaris teleius* (Bergsträsser) derived from the general aspects of the species biology, but without a solid experimental background. Theoretical studies also resulted in insightful recommendations that have not been tested in practice so far (Johst et al., 2006). Field studies on the effects of habitat management concerned the host *Myrmica* ants alone (Grill et al., 2008; Wynhoff et al., 2011). Therefore, we identified an urgent need for a field experiment that comprehensively explores the effects of habitat management on the butterflies, their host plant and host ants at one time. The only example of such a comprehensive investigation on *Phengaris* butterflies and host organisms was carried out in a non-experimental setting and thus did not result in specific recommendations for habitat management (Čámská et al., 2012).

In a management experiment in Western Hungary, we aimed to find an optimal timing and frequency of mowing in wet meadows inhabited by *P. teleius*, which is still widespread and abundant in the study region (Ábrahám, 2012). We intended to test the effects of mowing regimes with different timing and frequency, including cessation of mowing, on the components of a community-module

Table 1
Descriptive statistics of sampling in each study year. Mean values per squares are shown.

	2007				2010			
	Abandoned	Mowing in May	Mowing in May and September	Mowing in September	Abandoned	Mowing in May	Mowing in May and September	Mowing in September
Butterfly days	15	15	15	15	20	20	20	20
Captured butterflies	17.5	24.64	24.29	18.07	5.5	17.14	14.00	18.71
Daily butterfly numbers	1.17	1.64	1.62	1.21	0.28	0.86	0.70	0.94
S. officinalis flowerheads	147.36	845.07	644.86	129.07	60.14	1181.21	1047.07	547.43
Myrmica ant frequency	0.571	0.393	0.464	0.482	0.396	0.349	0.293	0.429

consisting of a parasitic butterfly, its host plant and host ant species. We tested economically feasible mowing regimes that may help to preserve the traditional land-use system (Plieninger et al., 2006), and can suppress the invasion of goldenrod.

2. Material and methods

2.1. Study species

The scarce large blue butterfly (*P. teleius*) is listed on the Annex II of Natura 2000 Habitats Directive. Despite its endangered status at the European scale (Van Swaay et al., 2010, 2012), it is one of the most widespread butterfly species in the area of the Őrség National Park (Ábrahám, 2012). Females deposit eggs into the flowerheads of the great burnet (*Sanguisorba officinalis* L.), where caterpillars develop for a few weeks by feeding on seeds. Larvae then descend to ground and await for being adopted by *Myrmica* ant workers (Thomas, 1984). After being carried into ant nests, caterpillars complete their development by predating on ant brood (Thomas et al., 1989). In Hungary, the primary host ant of *P. teleius* is *Myrmica scabrinodis* (Nyl.), although four additional species have been identified as its host (*Myrmica gallienii* (Bondroit), *M. salina* (Ruzsky), *M. specioides* (Bondroit), *Myrmica rubra* (L.)) (Tartally and Varga, 2008). The latter study reported caterpillars only from *M. scabrinodis* and *M. rubra* nests in our study region (Őrség National Park), but this finding was based on a very few *Myrmica* nests infested by *P. teleius* . The flight period of *P. teleius* is in July in our study sites, although its timing shows some variability across the region (Batáry et al., 2009; Kőrösi et al., 2012).

2.2. Study sites

We selected four meadows in the valley of Szentgyörgyvölgyi stream, Őrség National Park, Western Hungary (N46.75°, E16.35°, 210–230 m a.s.l.), all managed by the Őrség National Park Directorate. Meadows 1 and 2 were separated by ~200 m from each other at the upper reaches of the stream, while Meadows 3 and 4 were located ~5 km further downstream and ~200 m from each other (Fig. 1). These two pairs of meadows were formed by the land ownership of the NP. The vegetation on the upstream Meadows (1 and 2) was *Arrhenatherum* hay meadow and mesotrophic wet meadow on the downstream ones (3 and 4) (Király et al., 2001).

2.3. Experimental design

We divided all meadows into four plots of equal size that were managed differently. We applied three different mowing regimes, and kept a plot as a control, i.e., abandoned. The three regimes were: one cut per year in May one cut per year in September, and two cuts per year in both May and September. Management types were randomly assigned to the plots. Mowing has been carried out by RK-165 type drum mowers each year since May 2007. The hay was baled when dry and collected from the meadows within a month after mowing.

We surveyed the abundance of *P. teleius* and its host plant, and frequency of *Myrmica* ants in 2007 and 2010 following the same protocol. Within each management plot we designated four (on Meadows 1 and 2) or three (on Meadows 3 and 4) adjacent 20 × 20 m squares for butterfly counts (56 squares altogether; 4 × 4 in Meadows 1 and 2, 3 × 4 in Meadow 3 and 4) (Fig. A1 in online Appendix). We applied timed mark-recapture to assess butterfly abundance: in each square one surveyor spent five minutes thriving to capture, mark and release all *P. teleius* specimens. We sampled all meadows each day in a different sequence. We repeated these butterfly counts for several times to cover the whole flight season in July (Table 1). In the center of each square we designated a smaller, 10m × 10 m square in which we counted all flowerheads of the host plant once in the second half of the flight period. In those squares where host plant abundance was very high (i.e. >10 flowerheads m^{-2}), we counted the plants, randomly selected and counted the flowerheads on ten of them. Then the mean flowerhead number of those ten plants was multiplied by the number of plants to estimate flowerhead number. Within the 10m × 10 m squares, we also placed out baits on round plastic plates (8 cm diameter) on the ground in the early morning hours to sample *Myrmica* ants. Baits were regularly checked for 30 min and

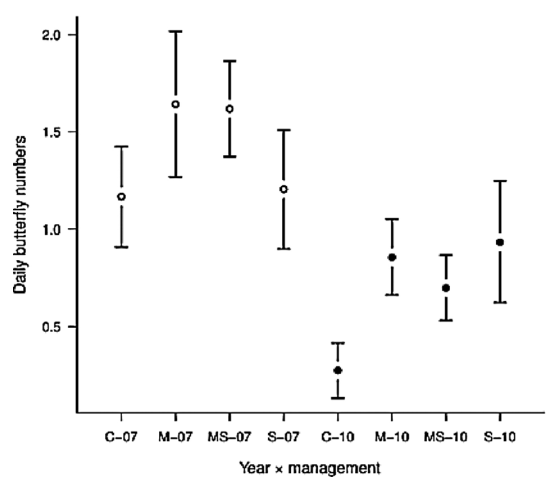

Fig. 2. Daily number of butterflies captured in each management type in 2007 and 2010. Error bars indicate 95% CIs. *C*: abandoned control, *M*: mowing in May; *MS*: mowing in May and September; *S*: mowing in September.

Table 2
Results of GLMMs on absolute numbers of response variables in both study years. Significant effects are in bold. We had two models for each response variable (year + year × management; management + year × management). Random effect denotes the proportion of variation explained by the random factor (meadow).

Response variable	Fixed effects	Estimation	SE	df	*t*-value	*p*-value	Random effect (%)
P. teleius daily numbers	Year 2010	−0.892	0.171	101	−5.225	<0.0001	<1
	Year 2007: mowing in May	0.476	0.171	101	2.791	0.006	
	Year 2010: mowing in May	0.582	0.171	101	3.411	<0.001	
	Year 2007: mowing in May and September	0.452	0.171	101	2.651	0.009	
	Year 2010: mowing in May and September	0.425	0.171	101	2.491	0.014	
	Year 2007: mowing in September	0.038	0.171	101	0.223	0.824	
	Year 2010: mowing in September	0.661	0.171	101	3.872	<0.001	
P. teleius daily numbers	Mowing in May	0.476	0.170	101	2.796	0.006	<1
	Mowing in May and September	0.452	0.170	101	2.656	0.009	
	Mowing in September	0.038	0.170	101	0.224	0.824	
	Control: year 2010	−0.892	0.170	101	−5.236	<0.0001	
	Mowing in May: year 2010	−0.786	0.170	101	−4.614	<0.0001	
	Mowing in May and September: year 2010	−0.919	0.170	101	−5.396	<0.0001	
	Mowing in September: year 2010	−0.269	0.170	101	−1.580	0.117	
S. officinalis flowerhead number	Year 2010	−0.896	0.636	101	−1.409	0.162	1
	Year 2007: mowing in May	1.747	0.371	101	4.708	<0.0001	
	Year 2010: mowing in May	2.978	0.549	101	5.420	<0.0001	
	Year 2007: mowing in May and September	1.476	0.379	101	3.890	<0.001	
	Year 2010: mowing in May and September	2.857	0.551	101	5.185	<0.0001	
	Year 2007: mowing in September	−0.133	0.501	101	−0.265	0.792	
	Year 2010: mowing in September	2.209	0.565	101	3.912	<0.001	
S. officinalis flowerhead number	Mowing in May	1.747	0.371	101	4.708	<0.0001	1
	Mowing in May and September	1.476	0.380	101	3.890	<0.001	
	Mowing in September	−0.133	0.501	101	−0.265	0.792	
	Control: year 2010	−0.896	0.636	101	−1.409	0.162	
	Mowing in May: year 2010	0.335	0.187	101	1.789	0.077	
	Mowing in May and September: year 2010	0.485	0.208	101	2.330	0.022	
	Mowing in September: year 2010	1.445	0.407	101	3.553	<0.001	
Myrmica frequency	Year 2010	−0.366	0.212	101	−1.728	0.087	80
	Year 2007: mowing in May	−0.375	0.212	101	−1.766	0.080	
	Year 2010: mowing in May	−0.127	0.238	101	−0.533	0.595	
	Year 2007: mowing in May and September	−0.208	0.202	101	−1.027	0.307	
	Year 2010: mowing in May and September	−0.303	0.250	101	−1.214	0.228	
	Year 2007: mowing in September	−0.170	0.200	101	−0.849	0.398	
	Year 2010: mowing in September	0.080	0.226	101	0.353	0.725	
Myrmica frequency	Mowing in May	−0.375	0.212	101	−1.766	0.080	80
	Mowing in May and September	−0.208	0.202	101	−1.027	0.307	
	Mowing in September	−0.170	0.200	101	−0.849	0.398	
	Control: year 2010	−0.366	0.212	101	−1.728	0.087	
	Mowing in May: year 2010	−0.118	0.238	101	−0.494	0.623	
	Mowing in May and September: year 2010	−0.461	0.242	101	−1.908	0.059	
	Mowing in September: year 2010	−0.116	0.215	101	−0.541	0.590	
S. gigantea cover	Year 2010	1.099	0.433	55	2.539	0.014	<1
	Year 2007: mowing in May	−0.111	0.545	55	−0.204	0.839	
	Year 2010: mowing in May	−0.919	0.405	55	−2.267	0.027	
	Year 2007: mowing in May and September	0.294	0.495	55	0.594	0.555	
	Year 2010: mowing in May and September	−3.350	1.175	55	−2.850	0.006	
	Year 2007: mowing in September	0.560	0.470	55	1.191	0.239	
	Year 2010: mowing in September	−0.547	0.357	55	−1.530	0.132	
S. gigantea cover	Mowing in May	−0.111	0.545	55	−0.204	0.839	<1
	Mowing in May and September	0.294	0.495	55	0.594	0.555	
	Mowing in September	0.560	0.470	55	1.191	0.239	
	Control: year 2010	1.099	0.433	55	2.539	0.014	
	Mowing in May: year 2010	0.291	0.524	55	0.556	0.580	
	Mowing in May and September: year 2010	−2.546	1.200	55	−2.122	0.038	
	Mowing in September: year 2010	−0.008	0.401	55	−0.019	0.985	

a few individuals were collected in ethanol for later identification. *Myrmica* ants were identified at species level. In 2007 we used four baits per square, whereas in 2010 we exposed nine baits per square in a grid with 3 m gaps. We used fish in oil mixed with honey as bait. Finally, percent cover of the invasive goldenrod (*S. gigantea*) was also estimated in the 10m × 10 m squares at the same time of host plant survey (it was relevant on Meadows 1 and 2 only).

2.4. Data analysis

We quantified *P. teleius* abundance by the sum of captured individuals in each square in a given study year. Butterflies captured more than once on the same day were counted at their first capture square. This means that each butterfly was counted as many times as (re)captured given that subsequent (re)captures

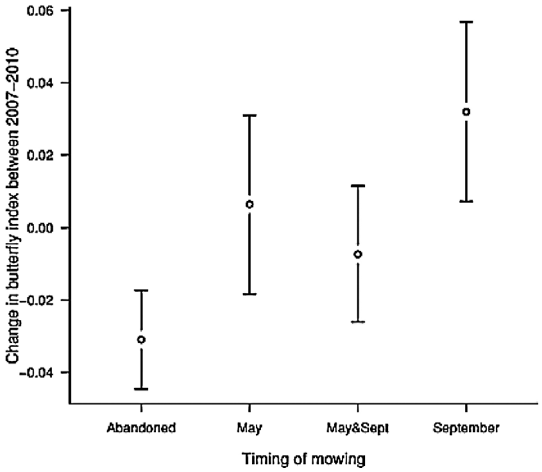

Fig. 3. Change of butterfly index between 2007 and 2010 in each management type. Error bars indicate 95% CIs.

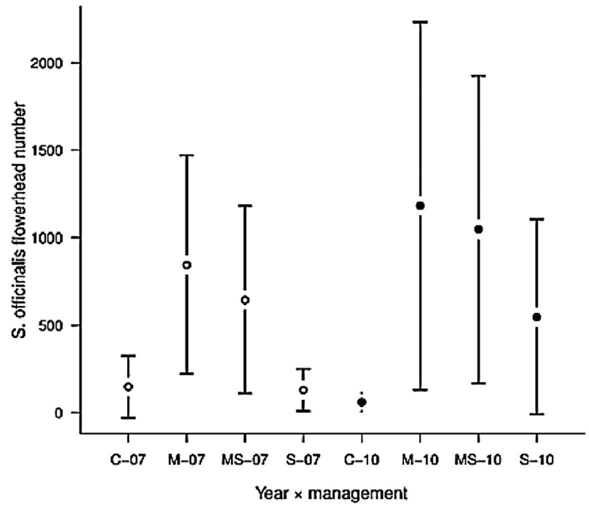

Fig. 4. Number of *S. officinalis* flowerheads in each management type in 2007 and 2010. Error bars indicate 95% CIs. *C*: abandoned control, *M*: mowing in May; *MS*: mowing in May and September; *S*: mowing in September.

happened on different days. We think this variable can properly characterize butterfly preferences for differently managed squares throughout the entire sampling season. To assess the effects of management on butterfly numbers we had to filter out the effects of year, meadow and their interaction, because population size of the butterfly may have annual fluctuations independently from management, and this fluctuation may differ among meadows. Moreover, the length of butterfly sampling period also varied between years. Thus we divided the sum of captures per squares by the sum of all captures in each meadow in a given year. In this way we obtained an index for each square ranging between 0 and 1 and summing up to one for each meadow, which is supposed to characterize the relative preference of squares by the butterfly. The change of this butterfly index between 2007 and 2010 in each square was used as a response variable. Additionally, we also used the mean daily number of butterflies captured in each square.

The number of host plant flowerheads showed a huge variation among meadows and among management types even at the beginning of the experiment (in 2007). Furthermore, the overall flowerhead number varied among years. Therefore, beside yearly absolute flowerhead numbers (NF_{2007}, NF_{2010}) and between-year difference in flowerhead numbers ($NF_{2010} - NF_{2007}$), we also used the proportional difference between years (NF_{2010}/NF_{2007}) as response variables.

To characterize host ant frequency, we used the proportion of baits that attracted *Myrmica* ants in each square in each year. The change of this proportion between 2007 and 2010 was used as a response variable. Most of the *Myrmica* species identified during the three years (*Myrmica gallienii*, *Myrmica salina*, *M. scabrinodis*, *Myrmica specioides*, *M. rubra*) are proven hosts of *P. teleius* (Tartally and Varga, 2008; Witek et al., 2008). However, in 2007 we found non-host *Myrmica* ants on three single baits (*M. sabuleti* in Meadow 1 and *M. schencki* and *M. vandeli* in Meadow 2). Finally, the difference in *Solidago gigantea* cover between 2007 and 2010 was also used as a response variable to study the effects of management.

To uncover the effects of management on each response variable we applied generalized linear mixed models (GLMM) with meadow as a random factor and management as a four-level fixed effect. We also constructed two models on real numbers of each response variable (mean daily number of butterflies, host plant flowerhead number, *Myrmica* frequency, *S. gigantea* cover) for both years (2007 and 2010). Fixed effects were year and year × management interaction in one model, and management and year × management interaction in the other. When diagnostic plots of models proved some violation of assumptions of the linear models (e.g., non-normal error distribution), we transformed the response variable and applied quasi-Poisson error distribution (changes in *Myrmica* frequency and *Solidago* cover were power-transformed, change of absolute flowerhead number was normalized). We also tested for correlations among *P. teleius* abundance, host plant flowerhead abundance, host ant frequency and *Solidago* cover in both 2007 and 2010. All analyses were performed using packages

Table 3
Estimated mean ± SEM of the change of each response variable between 2007 and 2010 in the four management types. *F* and *p* values of GLMMs are shown where available. Numerator DF was 3 in all models, while denominator DF was 28 in the *Solidago* model and 52 in all other models. We used normal error distribution in models of butterfly index and proportional change of host plant flowerhead number, while quasi-poisson error distribution in the rest of the models. Different letters indicate significant differences (*t* -test from summary table, $\alpha = 0.05$). Random effect denotes the proportion of variation explained by the random factor (meadow).

Variable	Abandoned control	Mowing in May	Mowing in September	Mowing in May and September	*F*	*p*	Random effect (%)
Change of butterfly index	-0.031 ± 0.009^{a}	0.037 ± 0.014^{b}	0.063 ± 0.014^{bc}	0.024 ± 0.014^{abd}	7.322	<0.001	<1
Absolute change of host plant flowerhead numbers	6.77 ± 0.21^{a}	0.39 ± 0.18^{b}	0.45 ± 0.18^{bc}	0.44 ± 0.18^{bcd}	N.A.	May: 0.034 September: 0.014 May and September: 0.016	<1
Proportional change of host plant flowerhead numbers	-1.20 ± 0.83^{a}	1.14 ± 1.02^{ab}	3.22 ± 1.02^{c}	0.95 ± 1.02^{abd}	3.53	0.021	8
Change of *Myrmica* frequency	-0.162 ± 0.080^{a}	0.201 ± 0.108^{ab}	0.144 ± 0.109^{abc}	0.005 ± 0.113^{abcd}	1.749	0.168	<1
Change of *Solidago* cover	0.215 ± 0.060^{a}	-0.183 ± 0.089^{b}	-0.196 ± 0.089^{bc}	-0.325 ± 0.093^{bcd}	4.291	0.013	<1

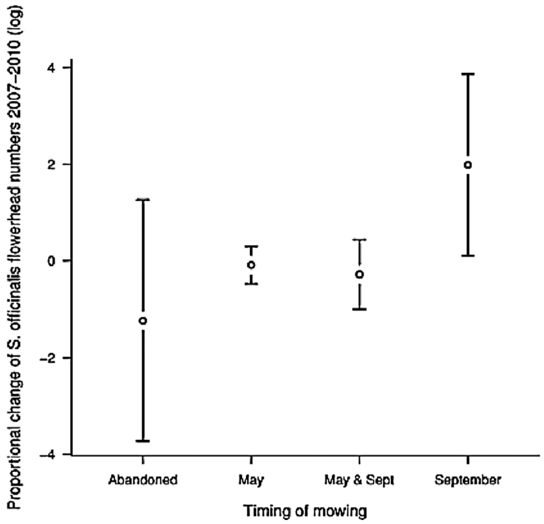

Fig. 5. Proportional change of *S. officinalis* flowerhead number between 2007 and 2010 in each management type. Error bars indicate 95% CIs.

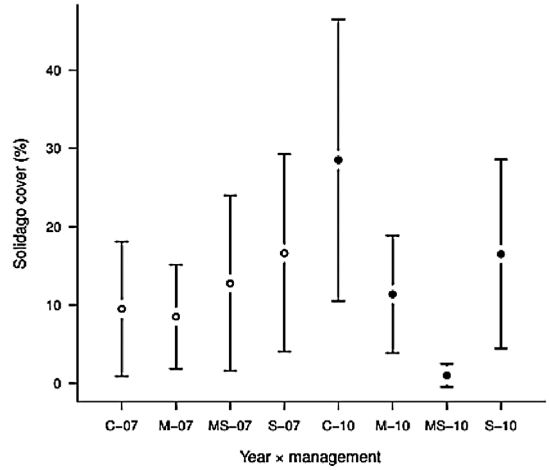

Fig. 7. *Solidago* cover in each management type in 2007 and 2010. Error bars indicate 95% CIs. *C*: abandoned control, *M*: mowing in May, *MS*: mowing in May and September, *S*: mowing in September.

lme4 (Bates et al., 2012) and nlme (Pinheiro et al., 2012) of the R 2.14.0 statistical software (R Development Core Team, 2012).

3. Results

Total and mean daily number of butterflies captured decreased from 2007 to 2010 (Table 1). Models on absolute butterfly abundance showed that in 2007 daily butterfly numbers were significantly higher in plots mown in May and in May and September than in abandoned plots, while in 2010 butterfly numbers were significantly higher in all management types than in abandoned plots. Moreover, by 2010 daily butterfly numbers significantly decreased in all management types except plots mown once in September (Fig. 2, Table 2). These results are concordant with the change of the butterfly index, which significantly increased in plots mown once a year in September compared to abandoned plots and plots mown twice per year (Fig. 3, Table 3). Furthermore, plots mown once a year in May were also preferred over abandoned plots, but there was no significant difference compared to plots mown once in September.

Total number of flowerheads increased between 2007 and 2010. Absolute flowerhead number in 2007 was significantly higher in plots mown in May and in May and September than in the abandoned plots, while in 2010 it was significantly higher in all managed plots than in the abandoned ones. Flowerhead number significantly increased between 2007 and 2010 in plots mown once in September and plots mown twice in May and September (Table 2, Fig. 4). Absolute change of flowerhead numbers between 2007 and 2010 was significantly higher in all management types than in abandoned plots. However, proportional change of flowerhead numbers was significantly higher only in plots mown once in September (Fig. 5, Table 3).

The change in the frequency of *Myrmica* ants between 2007 and 2010 showed very low variance among meadows and was not affected by management type (Table 3, Fig. A2 in online Appendix). The overall proportion of baits visited by *Myrmica* ants decreased during the study period (Table 1). Frequency of *Myrmica* species

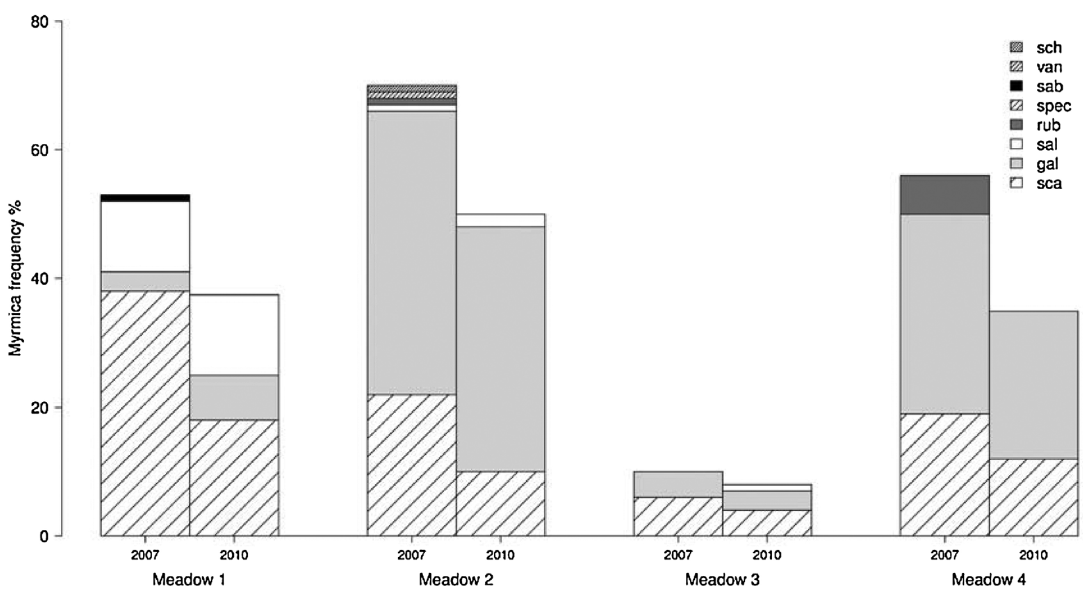

Fig. 6. Species composition of *Myrmica* assemblages in each meadow in each study year. Abbreviations of species names: sch: *M. schencki* ; van: *M. vandeli* ; sab: *M. sabuleti* ; spec: *M. specioides*; rub: *M. rubra*; sal: *M. salina*; gal: *M. gallienii*; sca: *M. scabrinodis*.

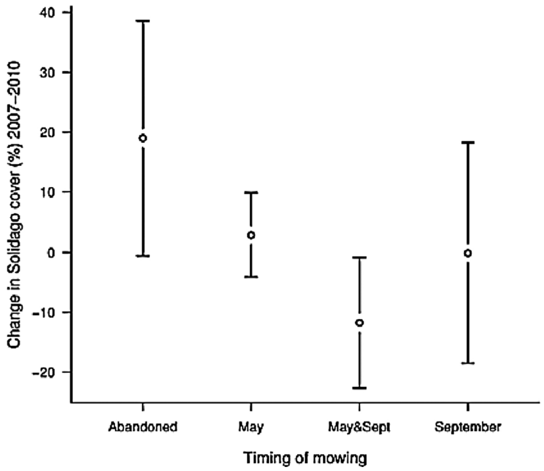

Fig. 8. Change of *Solidago* cover between 2007 and 2010 in each management type. Error bars indicate 95% CIs.

showed a considerable variance among meadows, but hardly changed over years, i.e., the species composition of *Myrmica* assemblages was stable in time (Fig. 6).

Management effect was significant on *Solidago* cover (in Meadows 1 and 2) (Table 2). In 2007, *Solidago* cover did not differ significantly among the four management types. By 2010, it significantly increased in abandoned plots, and became significantly lower in plots mown in May and in May and September than in abandoned plots. However, it showed a significant decrease during the three years only in plots cut twice per year (Tables 2, 3, Figs. 7, 8).

Finally, we found significant positive correlation between *P. teleius* and host plant flowerhead abundances in both years, and significant negative correlation between host plant flowerhead abundance and host ant frequency in 2010 (Table 4). *Solidago* cover did not correlate with any other variables. Fig. 9 demonstrates that proportional change in the number of host plant flowerheads and change in the butterfly index are positively correlated. However, this relationship is confounded by the effect of management, thus no statistical test was performed.

4. Discussion

In this study we found significant effects of timing and frequency of mowing on the habitat use of the scarce large blue butterfly and on the abundance of its larval host plant. To our best knowledge, this is the first attempt to explicitly test the effects of different grassland management schemes on the habitat use of a large blue butterfly in practice, although *Phengaris* (*Maculinea*) species have been the focus of considerable research effort in the last few decades (e.g., Settele et al., 2005; Thomas et al., 2009; Settele and Kühn, 2009). In spite of the short duration of our study, we found statistically significant and/or qualitatively informative effects of management on the interacting species examined.

4.1. Management effects on butterfly abundance

P. teleius butterflies mostly preferred plots cut once a year in September. This was the only management type under which daily number of butterflies did not decrease significantly from 2007 to 2010, and where butterfly index showed the highest increase. This is concordant with the change in the number of *S. officinalis* flowerheads, which showed the highest proportional increase in plots mown once in September. In most meadows the initial number of host plant flowerheads was very low in the “September plots”, which means that increase of flowerhead abundance affected butterflies most positively at low initial host plant abundance. These results are in agreement with previous findings, namely that at low density of *S. officinalis* , density of *P. teleius* is positively correlated with it (Batáry et al., 2007; Dierks and Fischer, 2009), while above a threshold host plant density does not correlate with butterfly density (Nowicki et al., 2007). Although, higher butterfly index does not obviously reflect to higher carrying capacity, it can rather be a result of that adult butterflies stay for longer in certain patch types (e.g., Ouin et al., 2004).

Our finding that *P. teleius* butterflies avoided abandoned plots and showed clear preferences toward less intensively managed plots even at a small spatial scale is in agreement with previous results. In wet meadows in Poland, Skórka et al. (2007) demonstrated that cessation of mowing may lead to the invasion of reed and goldenrod and hence a deterioration of butterfly habitats, while extensively mown meadows and fallow lands were highly preferred by butterflies. They also showed that the presence and relative abundance of *P. teleius* were good indicators of general butterfly species richness in wet grasslands. In a mountain pastoral landscape in Spain, Dover et al. (2011a) revealed that the early stages of abandonment may be beneficial for butterflies, but lack of management on the long-term causes severe loss of species. Bergman and Kindvall (2004) also demonstrated that abandonment of grazing or mowing in meadows threatened the long-term survival of *Lopinga achine* in Sweden. Although management history of our study sites is not fully known, our results suggest that even a short-term (3 years) abandonment can turn habitats less preferable for *P. teleius,* and therefore may lead to its local extinction.

Number of butterflies marked per day was remarkably lower in 2010 than in 2007. This does not indicate, however, a declining trend in the population size. The four meadows sampled in our study are parts of a mosaic landscape comprising many differently managed grassland patches. This landscape is occupied by an extant metapopulation of *P. teleius* (Batáry et al., 2009). The sampled meadows were either adjacent to or in the vicinity of other meadows, thus they could not be considered as demographically independent and representative units of the whole metapopulation.

4.2. Management effects on host plant abundance

The difference in total flowerhead numbers between 2007 and 2010 is mostly a result of that it increased in some squares from ~2500 to ~4000 in Meadow 4. From a butterfly viewpoint, such an increase is irrelevant, because even 10 flowerheads m^{-2} represent

Table 4
Kendall's tau correlation coefficients among butterfly and host plant abundance, *Solidago* cover and host ant frequency. Significant values are in bold.

		2007	2010
P. teleius abundance	*S. officinalis* flowerhead number	**0.27**	**0.32**
P. teleius abundance	Host ant frequency	−0.09	0.01
P. teleius abundance	*Solidago* cover	−0.09	0.02
S. officinalis flowerhead number	Host ant frequency	−0.19	**−0.26**
S. officinalis flowerhead number	*Solidago* cover	0.13	−0.01
Host ant frequency	*Solidago* cover	0.07	0.16

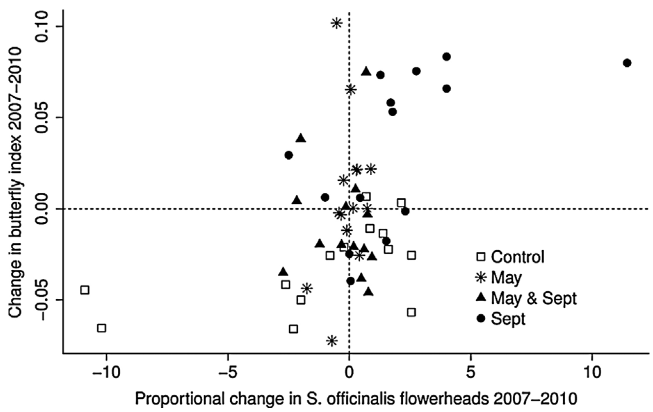

Fig. 9. Relationship between the change of the butterfly index and proportional change of *S. officinalis* flowerhead number.

unlimited resources for oviposition and early larval development of *P. teleius* (Thomas, 1984; Nowicki et al., 2007). Increase of flowerhead numbers is more important in those squares where initial host plant density was close to zero. The number of *S. officinalis* flowerheads increased in plots mown once in September in all meadows. According to Fan et al. (2003), *S. officinalis* tolerates an intermediate level of stress and disturbance. In Meadows 1 and 2, which are more xeric and vulnerable to desiccation, mowing in May might result in a too short turf height and too dry microclimatic conditions in summer implying a high level of water stress for *S. officinalis* . In these meadows, mowing once a year in September may prevent the succession of the vegetation in the long-term, but also keep the sward tall and dense enough for summer to prevent the desiccation of the soil, thus providing intermediate stress and disturbance. In the more humid Meadows 3 and 4, summer drought does not seem to limit the growth of *S. officinalis* . In these meadows the three mowing regimes tested are equivalently good in suppressing the invasion of sedges and guarantee a good habitat for *S. officinalis* .

4.3. Management effects on host ants

The frequency of *Myrmica* host ants was not affected by management in our study. Proportion of baits visited by *Myrmica* ants was 40–70% in all meadows (except Meadow 3), and management effect could not be detected on any of the meadows. These results seemingly contradict to Grill et al. (2008), who found that once a year mowing in September was the most beneficial for *Myrmica* hosts of *P. teleius* in Germany. They operated with comparable plot sizes and bait numbers to ours, but they used ant abundance as a response variable and their results were not statistically robust enough (see details in Grill et al. (2008)). Wynhoff et al. (2011) also revealed a significant effect of management on the abundance, but not occupancy of *Myrmica* ants in the Netherlands. Therefore, our results do not strikingly contradict to others, since we used a metric of occupancy of *Myrmica* ants instead of abundance. According to Lenda et al. (2013) in meadows invaded by invasive goldenrods, *Myrmica* workers can travel for longer distances from their nests to find food than in meadows with native vegetation. Hence, by using baits we may have introduced some bias in our analysis. Since we did not count *Myrmica* nests, we were unable to distinguish between the non-significant effect of management regime and potential higher mobility of ant workers in deteriorated habitats.

By applying different mowing regimes within the meadows, we created different microhabitats for both the host plant and the butterfly. We suppose that parasitic pressure on *Myrmica* ant colonies were higher in plots preferred by both *S. officinalis* and *P. teleius*, while plots providing unfavorable conditions for the host plant and the butterfly may have served as refuge areas for *Myrmica* colonies. From these refuge areas, due to the small-scale heterogeneity of management, *Myrmica* ants could have permanently and instantaneously recolonized those plots that were more strongly parasitized by *Phengaris* butterflies (Thomas et al., 1997). In other words, management had probably a double effect on *Myrmica* ants as it potentially influenced the microclimatic conditions and food supply through modifying vegetation structure (Dahms et al., 2005; Dauber et al., 2006), but it also affected the parasitic pressure on ant colonies. These two effects could neutralize each other.

An experimental period of three years might be too short to detect changes in relative frequencies of host *Myrmica* ants. This is also supported by the fact that species composition and dominance ranking of *Myrmica* assemblages at a meadow scale rarely changed over the study years (Fig. 6), though our data were not sufficient for a detailed analysis of species composition. Differences among meadows also showed low temporal variability. These are in agreement with findings of Dahms et al. (2005) who could not reveal any impact of management type on species richness and composition of ant communities in Germany. Furthermore, Dauber et al. (2006) revealed that the historically continuously managed grassland sites can harbour species-rich ant communities and that afforestation due to abandonment is the most important factor affecting ant community composition. Elmes et al. (1998) also stressed that ant communities can significantly change within ten years if meadows are encroached by trees and bushes due to abandonment. Therefore, the lack of management effect in our case may be due to the small difference among management types and short duration of the experiment.

4.4. Management effects on the invasive goldenrod

We found that the invasive goldenrod *S. gigantea* could be successfully suppressed by two cuts per year, one cut per year (either in May or in September) can stop the invasion at best. *S. gigantea* was present in Meadows 1 and 2 that were less humid than Meadows 3 and 4. In the latter ones, the advancement of sedges was observed, especially in the abandoned plots. Sedges may also supersede herbs such as *S. officinalis,* and their encroachment may result in species poor plant communities.

4.5. Implications for conservation

We conclude that cessation of mowing can rapidly lead to the decline of habitat quality for *P. teleius* due to the invasion of sedges and/or goldenrod, and in some cases due to the decrease of host plant abundance as well. This is in agreement with earlier findings in Central Europe (Skórka et al., 2007). In our study region, wet meadows are likely to harbor high densities of *S. officinalis* ($5 <$ flowerheads m^{-2}) and in such meadows either type of mowing that we tested seem appropriate for the long-term preservation of *P. teleius* populations. In more xeric meadows with low abundance of host plant, the optimal management type is one cut per year in September, complemented with additional selective cutting of *S. gigantea* patches. The fact that mowing in May was not significantly worse for *P. teleius* than mowing in September is of outstanding importance from a practical conservation point of view. Although late mowing has been traditionally preferred by conservation practitioners, it is not economical because of poorer hay quality, and is therefore refused by farmers (Szentirmai pers. comm.) Our results indicate that early mowing could be a good compromise between the interests of conservation and farmers. We did not find a best type of management for host *Myrmica* ants, but one cut per year in autumn was found the best option for the maintenance of host *Myrmica* ants in the Netherlands (Wynhoff et al., 2011). If the aim of nature conservation is to improve the quality and increase the carrying capacity of local habitat patches, then, according to the recommendations of the vast majority of the literature, habitat management should be optimized for the host ant populations (e.g., Anton et al., 2008; Thomas et al., 2009). We note that a disadvantage of regular late mowing may be that nutrients are not removed from the sites allowing shrubs and tall herbs to overgrow the host plants (Wynhoff et al., 2011). Therefore, we suggest that a small-scaled, mosaic-like pattern of diverse mowing regimes would be most beneficial for the long-term preservation of *P. teleius* populations and species-rich insect communities in the study region (see also Cizek et al., 2012).

In this study we tested mowing regimes such that comply with the current laws of Hungary and can be economically realistic. However, theoretical studies suggested that less intensive management regimes, for example mowing in every second or third year, would be beneficial for the long-term persistence of *P. teleius* (Johst et al., 2006) and would be financially feasible with compensation payments (Drechsler et al., 2007). Therefore, it would be worthwhile to test the effects of such less intensive management types in those areas of the Őrség region which are dedicated for nature conservation and are not threatened by the invasion of goldenrod. Moreover, the effects of grazing on *Phengaris* habitats should be also studied, because livestock husbandry of traditional varieties can be an appropriate alternative for habitat management (e.g., Dolek and Geyer, 1997; Saarinen and Jantunen, 2005; Pöyry et al., 2005; Öckinger et al., 2006). Finally, if *P. teleius* is proved to be a useful indicator species of high biodiversity (e.g., Skórka et al., 2007; Spitzer et al., 2009), then management of wet grasslands could be tailored to the needs of this butterfly in the Őrség region where it is still widespread (Ábrahám, 2012). Our study could clearly form the fundamentals of designing such a regional nature conservation management plan.

Acknowledgements

We thank Ádám Balogh, László Bokor, Gábor Csontos, Gergely Kecskeméti and Nóra Ragasits for their help in the field work. We are grateful to Sándor Csősz for the identification of *Myrmica* ants. We are indebted to two anonymous reviewers whose suggestions and comments helped us to improve the manuscript. This study was carried out within the framework of grassland management research programme of the Őrség National Park Directorate. The study was conducted in cooperation with the Hungarian Lepidopterological Society and complies with the laws of Hungary. PB was supported by the German Research Foundation (DFG BA 4438/1-1).

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.2014.06.019.

References

Anton, C., Musche, M., Hula, V., Settele, J., 2008. *Myrmica* host-ants limit the density of the ant-predatory large blue *Maculinea* nausithous. J. Insect Conserv. 12, 511–517.
Ábrahám, L., 2012. Butterfly Atlas. Őrség-Goričko. Őrségi Nemzeti Park Igazgatóság, Őriszentpéter.
Báldi, A., Batáry, P., 2011. The past and future of farmland birds in Hungary. Bird Study 58, 365–377.
Batáry, P., Kőrösi Á, Örvössy, N., Kövér, S., Peregovits, L., 2009. Species-specific distribution of two sympatric *Maculinea* butterflies across different meadow edges. J. Insect Conserv. 13, 223–230.
Batáry, P., Örvössy, N., Kőrösi Á, Vályi Nagy, M., Peregovits, L., 2007. Microhabitat preferences of *Maculinea teleius* (Lepidoptera: Lycaenidae) in a mosaic landscape. Eur. J. Entomol. 104, 731–736.
Bates, D., Maechler, M., Bolker, B., 2012. lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-0. http://CRAN.R-project.org/package=lme4.
Bergman, K.-O., Kindvall, O., 2004. Population viability analysis of the butterfly *Lopinga achine* in a changing landscape in Sweden. Ecography 27, 49–58.
Čámská, K., Pavlásek, J., Bezděčka, P., Bezděčková, K., Hadincová, V., Bauer, P., 2012. Effect of different grassland management on populations of two endangered Phengaris butterflies and their host organisms. Poster. The 8th European Conference on Ecological Restoration, September 9–14, České Budějovice, Czech Republic.
Cizek, O., Zamecnik, J., Tropek, R., Kocarek, P., Konvička, M., 2012. Diversification of mowing regimes increases arthropods diversity in species-poor cultural hay meadows. J. Insect Conserv. 16, 215–226.
Cremene, C., Groza, G., Rákosy, L., Schileyko, A.A., Baur, A., Erhardt, A., Baur, B., 2005. Alterations of steppe-like grasslands in Eastern Europe: a threat to regional biodiversity hotspots. Conserv. Biol. 19, 1606–1618.
Dahms, H., Wellstein, C., Wolters, V., Dauber, J., 2005. Effects of management practices on ant species richness and community composition in grasslands (Hymenoptera: Formicidae). Myrmecol. Nachr. 7, 9–16.
Dauber, J., Bengtsson, J., Lenoir, L., 2006. Evaluating effects of habitat loss and land-use continuity on ant species richness in seminatural grassland remnants. Conserv. Biol. 20, 1150–1160.
de Groot, M., Kleijn, D., Jogan, N., 2007. Species groups occupying different trophic levels respond differently to the invasion of semi-natural vegetation by *Solidago canadensis*. Biol. Conserv. 136, 612–617.
Dierks, A., Fischer, K., 2009. Habitat requirements and niche selection of *Maculinea nausithous* and *M. teleius* (Lepidoptera: Lycaenidae) within a large sympatric metapopulation. Biodivers. Conserv. 18, 3663–3676.
Dolek, M., Geyer, A., 1997. Influence of management on butterflies of rare grassland ecosystems in Germany. J. Insect Conserv. 1, 125–130.
Dover, J.W., Rescia, A., Fungariño, S., Fairburn, J., Carey, P., Lunt, P., Arnot, C., Dennis, R.L.H., Dover, C.J., 2011a. Land-use, environment, and their impact on butterfly populations in a mountainous pastoral landscape: individual species distribution and abundance. J. Insect Conserv. 15, 207–220.
Dover, J.W., Spencer, S., Collins, S., Hadjigeorgiou, I., Rescia, A., 2011b. Grassland butterflies and low intensity farming in Europe. J. Insect Conserv. 15, 129–137.
Drechsler, M., Wätzold, F., Johst, K., Bergmann, H., Settele, J., 2007. A model-based approach for designing cost-effective compensation payments for conservation of endangered species in real landscapes. Biol. Conserv. 140, 174–186.
Elmes, G.W., Thomas, J.A., Wardlaw, J.C., Hochberg, M.E., Clarke, R.T., Simcox, D. J., 1998. The ecology of *Myrmica* ants in relation to the conservation of *Maculinea* butterflies. J. Insect Conserv. 2, 67–78.
Fan, J.P., Zhong, H.P., Liang, B., Du, Z.C., 2003. A study on competition among perennial ryegrass and six other species in different conditions of stress and disturbance. Acta Phytoecol. Sinica 4, 014.
Grill, A., Cleary, D.F.R., Stettmer, C., Bräu, M., Settele, J., 2008. A mowing experiment to evaluate the influence of management on the activity of host ants of *Maculinea* butterflies. J. Insect Conserv. 12, 617–627.
Johst, K., Drechsler, M., Thomas, J.A., Settele, J., 2006. Influence of mowing on the persistence of two large blue butterfly species. J. Appl. Ecol. 43, 333–342.
Király, G., Mesterházy, A., Király, A., 2001. Habitat map of the Őrség Special Area of Conservation (HUON8). Őrség National park Directorate, Őriszentpéter, pp. 2011.
Kleijn, D., Kohler, F., Báldi, A., Batáry, P., Concepción, E.D., Clough, Y., Diaz, M., Gabriel, D., Holzschuch, A., Knop, E., Kovács, A., Marshall, E.J.P., Tscharntke, T., Verhulst, J., 2009. On the relationship between farmland biodiversity and land-use intensity in Europe. Proc. R. Soc. B 276, 903–909.
Kőrösi, Á., Örvössy, N., Batáry, P., Harnos, A., Peregovits, L., 2012. Different habitat selection by two sympatric *Maculinea* butterflies at small spatial scale. Insect Conserv. Divers. 5, 118–126.
Lenda, M., Witek, M., Skórka, P., Moron, D., Woyciechowski, M., 2013. Invasive alien plants affect grassland ant communities, colony size and foraging behaviour. Biol. Invasions 15, 2403–2414.
Nilsson, S.G., Franzén, M., Jonsson, E., 2008. Long-term land-use changes and extinction of specialised butterflies. Insect Conserv. Divers. 1, 197–207.
Nowicki, P., Pepkowska, A., Kudlek, J., Skórka, P., Witek, M., Settele, J., Woyciechowski, M., 2007. From metapopulation theory to conservation recommendations: lessons from spatial occurrence and abundance patterns of *Maculinea* butterflies. Biol. Conserv. 140, 119–129.
Ouin, A., Aviron, S., Dover, J., Burel, F., 2004. Complementation/supplementation of resources for butterflies in agricultural landscapes. Agric. Ecosyst. Environ. 103, 473–479.
Öckinger, E., Eriksson, A.K., Smith, H.G., 2006. Effects of grassland abandonment, restoration and management on butterflies and vascular plants. Biol. Conserv. 133, 291–300.
Pinheiro, J., Bates, D., DebRoy S., Sarkar, D., R Development Core Team, 2012. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-105.
Plieninger, T., Hochtl, F., Spek, T., 2006. Traditional land-use and nature conservation in European rural landscapes. Environ. Sci. Policy 9, 317–321.

Pöyry, J., Lindgren, S., Salminen, J., Kuussaari, M., 2005. Responses of butterfly and moth species to restored grazing in semi-natural grasslands. Biol. Conserv. 122, 465–478.
R Development Core Team, 2012. R a language and environment for statistical computing. http://www.r-project.org.
Rescia, A., Pons, A., Lomba, I., Esteban, C., Dover, J.W., 2008. Reformulating the social-ecological system in a cultural rural mountain landscape in the Picos de Europa region (northern Spain). Landsc. Urban Plan. 88, 23–33.
Rösch, V., Tscharntke, T., Scherber, C., Batáry, P., 2013. Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities. J. Appl. Ecol. 50, 387–394.
Saarinen, K., Jantunen, J., 2005. Grassland butterfly fauna under traditional animal husbandry: contrasts in diversity in mown meadows and grazed pastures. Biodivers. Conserv. 14, 3201–3213.
Schmitt, T., Rákosy, L., 2007. Changes of traditional agrarian landscapes and their conservation implications: a case study of butterflies in Romania. Divers. Distrib. 13, 855–862.
Schmitz, M.F., De Aranzabal, I., Aguilera, P., Rescia, A., Pineda, F.P., 2003. Relationship between landscape typology and socioeconomic structure–scenarios of change in Spanish cultural landscapes. Ecol. Model. 168, 343–356.
Settele, J., Kühn, E., 2009. Insect conservation. Science 325, 41–42.
Settele, J., Kühn, E., Thomas, J.A., 2005. Studies on the ecology and conservation of butterflies in Europe. Vol. 2: Species ecology along a European gradient: Maculinea butterflies as a model. Pentsoft Sofia.
Skórka, P., Lenda, M., 2010. Abandoned fields as refuges for butterflies in agricultural landscapes of Eastern Europe. In: Harris, E.L., Harris, E.L., Davies, N.E., Davies, N. E. (Eds.), Insect Habitats: Characteristics, Diversity and Management. Nova Science Publishers, New York, pp. 83–103.
Skórka, P., Settele, J., Woyciechowski, M., 2007. Effects of management cessation on grassland butterflies in southern Poland. Agric. Ecosyst. Environ. 121, 319–324.
Spitzer, L., Benes, J., Dandova, J., Jaskova, V., Konvicka, M., 2009. The large blue butterfly, Phengaris *Maculinea arion* , as a conservation umbrella on a landscape scale: the case of the Czech Carpathians. Ecol. Indic. 9, 1056–1063.
Stefanescu, C., Penuelas, J., Filella, I., 2009. Rapid changes in butterfly communities following the abandonment of grasslands: a case study. Insect Conserv. Divers. 2, 261–269.
Stenseke, M., 2006. Biodiversity and the local context: linking seminatural grasslands and their future use to social aspects. Environ. Sci. Pol. 9, 350–359.
Stoate, C., Báldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., de Snoo, G.R., Rákosy, L., Ramwell, C., 2009. Ecological impacts of early 21st century agricultural change in Europe – a review. J. Environ. Manage. 91, 22–46.
Tartally, A., Varga, Z., 2008. Host ant use of *Maculinea teleius* in the Carpathian Basin (Lepidoptera: Lycaenidae). Acta Zool. Acad. Sci. Hung. 54, 257–268.
Thomas, J.A., 1984. The behaviour and habitat requirements of *Maculinea nausithous* (the Dusky Large Blue butterfly) and *Maculinea teleius* (the Scarce Large Blue) in France. Biol. Conserv. 28, 325–347.
Thomas, J.A., Elmes, G.W., Clarke, R.T., Kim, K.G., Munguira, M.L., Hochberg, M.E., 1997. Field evidence and model predictions of butterfly-mediated apparent competition between Gentian plants and red ants. Acta Oecol. 18, 671–684.
Thomas, J.A., Elmes, G.W., Wardlaw, J.C., Woyciechowski, M., 1989. Host specificity among *Maculinea* butterflies in *Myrmica* ant nests. Oecologia 79, 452–457.
Thomas, J.A., Simcox, D.J., Clarke, R.T., 2009. Successful conservation of a threatened *Maculinea* butterfly. Science 325, 80–83.
Thomas, J.A., Simcox, D.T., Hovestadt, T., 2011. Evidence based conservation of butterflies. J. Insect Conserv. 15, 241–258.
Van Swaay, C.A.M., 2013. The European Grassland Butterfly Indicator: 1990–2011. Technical Report. European Environment Agency, Luxembourg.
Van Swaay, C.A.M., Collins, S., Dušej, G., Maes, D., Munguira, M.L., Rákosy, L., Ryrholm, N., Šašić, M., Settele, J., Thomas, J.A., Verovnik, R., Verstrael, T., Warren, M., Wiemers, M., Wynhoff, I., 2012. Dos and donts for butterflies of the Habitats Directive of the European Union. CNat. Conserv. 1, 73–153.
Van Swaay, C.A.M., Cuttelod, A., Collins, S., Maes, D., Munguira, M.L., Šašić, M., Verovnik, R., Verstrael, T., Warren, M.S., Wiemers, M., Wynhoff, I., 2010. European red list of butterflies. Publications Office of the European Union, Luxembourg.
Witek, M., Sliwinska, E.B., Skórka, P., Nowicki, P., Wantuch, M., Vrabec, V., Settele, J., Woyciechowski, M., 2008. Host ant specificity of large blue butterflies Phengaris (*Maculinea*) (Lepidoptera: Lycaenidae) inhabiting humid grasslands in East-central Europe. Eur. J. Entomol. 105, 871–877.
Wynhoff, I., van Gestel, R., van Swaay, C.A.M., van Langevelde, F., 2011. Not only the butterflies: managing ants on road verges to benefit Phengaris (*Maculinea*) butterflies. J. Insect Conserv. 15, 189–206.