

Restoration of subalpine species-rich grasslands: short-term vs long-term changes in the density and diversity of above-ground insects

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ABSTRACT

Due to decrease in the area of extensively managed, semi-natural grasslands, that contribute to high biodiversity level preservation, the conversion of highly productive meadows to extensively managed, species-rich grasslands is now regarded as an important task for nature conservation. The aim of this long-term study was to assess the significance of restoration measures for diversity and trophic structure of above-ground insect community. That study challenges some weaknesses of previous studies as it was conducted with the use of suction trap enabling quantitative analyses of the changes in most insect taxa, and in a long time-span (1992–2005) in a set of permanent plots. The study area was located in a subalpine zone in Bavaria, near Laufen (Germany). The restoration process was initiated in 1996 by a cessation of fertilization and reduction of number of mowing to 1–2 per year. The changes in insect density and diversity (number of families) were monitored in ten restored and two reference plots with the aid of a suction trap. The changes in the insect community recorded during 14 years support findings from other studies that response of insect community to restoration process is usually slow on average. The short-term comparison in 2004–2005 between the restored and reference plots show that the first ones were characterized by more diverse (in term of family number) insect communities (as a whole as well as in guilds of predatory and parasitic species). From the other side, the long-term trend analysis shows that since 1998–2000 insect diversity and abundance was declining. Also trophic structure is fluctuating without clearly defined trend. These findings are in line with the results of the analyses of taxonomic composition similarity. They did not support the expectations neither that difference between initial and current taxonomical composition in a restored plot increases in time (mainly because of incoming new species), nor that spatial heterogeneity of insect assemblages should increase. However, spatio-temporal insect interactions between sample plots (located close to each other), linked to high movement ability of many insect taxa, could mask the changes in insect community caused by restoration.

INTRODUCTION

The biodiversity of agricultural areas depends strongly on the presence of semi-natural, extensively managed grasslands (Poschlod and Wallis-DeVries 2002). For example, many endangered species, e.g. birds and

vascular plants, are characteristic for wet grasslands (Bakker and Berendse 1999, Woodcock *et al.* 2006, Liira *et al.* 2008). It has been shown in several studies that extensively used grasslands are more favourable for many taxonomic groups than the ones that are intensively used (e.g., for auchenorrhynchs

– Andrzejewska 1991; for carabid beetles – Brose 2003; for butterflies – Dolek and Geyer 1997; for birds – Olsen and Schmidt 2004; for grasshoppers – Nentwig *et al.* 1999). As a consequence, extensive management of grasslands is one of the main tools for biodiversity conservation in Europe (Bakker 1989, Bignal and McCracken 1996, van Diggelen *et al.* 2005).

Grassland management in Europe has been changing considerably for the last 50 years (Stoate *et al.* 2009). Extensive farming dominated up to the 1950s. Since then, most grassland areas have either been improved (i.e. fertilized and cut for hay or silage several times a year) or their management has been stopped for economic reasons (Groombridge 1992, Strijker 2005), and they are gradually overgrown by woody plants. As a result, grassland area has decreased (Poschlod *et al.* 2005) and the populations of some species associated with them have also declined. The restoration of species-rich, extensively managed grasslands is therefore an important task for conservation and has been the subject of numerous ecological studies (for review see Littlewood *et al.* 2012).

However, most studies had some drawbacks. Firstly, the invertebrates were monitored mostly with the aid of pitfall traps, despite strong criticism of that method used as tool for monitoring insect abundance (Lang 2000). Secondly, some studies show that complete restoration can only be achieved after many decades, if ever (e.g., for vegetation – Bakker and Berendse 1999, Walker *et al.* 2004, Poptcheva *et al.* 2009; for Auchenorrhyncha – Nickel and Achtziger 2005; for carabid beetles – Van Dijk 1986). Thirdly, some taxa respond faster, others – slower (Woodcock *et al.* 2008), and the differences may be highlighted by the landscape features (Woodcock *et al.* 2010, Knop *et al.* 2011). Due to a long time needed for reliable assessment of the changes during restoration process, some researchers have used a “space-for-time substitute” approach, i.e. had compared at the same time the studied communities between the sample plots, which represented various stages of changing grasslands. This approach significantly reduces the duration of the fieldwork as it is based on short-term comparison between some plots, which dif-

fer in the date of restoration, but its results may be seriously biased due to the differences in habitat quality between sampling plots (Poptcheva *et al.* 2009, Rácz *et al.* 2013). Finally, in most cases, especially in zoological studies, only few species or selected groups of species have been studied, so the conclusions could be biased by specificity of taxa used for the analyses.

Here, we present results of a study on long-term changes in above-ground insect communities related to the changes in grassland vegetation under restoration process. That study challenged some of weaknesses mentioned above as: (i) suction trap enabling quantitative, reliable sampling of most insect taxa (Brook *et al.* 2008) was used, and (ii) it was carried out in long time-span (1992–2005) in a set of permanent plots.

The aim of the study was to recognize a pattern of changes in the insect community related to management extensification with respect to abundance and taxonomic and trophic diversity. Applied scheme of sampling enabled verifying: a) how consistent the pattern of changes in insect community across trophic guilds is, b) which guilds benefit from the management extensification more than others, and c) whether the general insect diversity of the area has responded to restoration measures.

The data gathered in this project have been used earlier to summarize the results, however the analyses were performed on basis of shorter period, only most general features of insect community (total biomass and diversity index) were considered or only few species have been selected for analysis (Mannhart *et al.* 2004, Sachteleben *et al.* 2007).

Considering that intensive grassland management decreases species richness and abundance, especially strongly in case of specialized predatory and parasitic species (Albrecht *et al.* 2007), we expected that extensification of management practices would result in:

- a) increase in overall taxonomic diversity (number of families) and insect abundance,
- b) increase in functional diversity as reflected by more even share of trophic guilds,
- c) increase in spatial diversification of insect community (i.e. beta-diversity).

First assumption is related mainly to lower insect mortality and less frequent damages

of habitat (due to smaller number of cuts), second one – to increase of parasitic and predatory insects share in community, and third one – to increase in spatial diversification of insects communities (due to more stable conditions and cessation of fertilization, that could allow persistence and increase in abundance of highly specialized, K-strategy species).

STUDY AREA

The study was conducted at the Ecological Field Station of the Bavarian Academy for Nature Conservation and Land Care in Laufen, Germany (47°94'N, 12°89'E). The station is located in the subalpine zone in south-eastern Bavaria (for a detailed description, see Manhart *et al.* 2003). The climate is mild oceanic, with an annual rainfall of 1000–1400 mm,

and an annual mean temperature of 7.5–10°C. The relatively low altitude (c. 400 m above sea level) and occurrence of foehn winds result in more than 40 summer days per year.

The study was carried out in mosaics of small patches (called “plots” in later parts of the text) of various vegetation types, mostly grasslands and tall-herb communities, located in a brook valley (Schinderbach). Grassland communities prevailed in the plots that were managed intensively between 1950 and 1970. They were improved by mineral and organic fertilization each year and regularly cut for silage up to five times per year and two-three times per year in 1989–1995 (Manhart *et al.* 2004). At the same time, tall-herb communities developed in areas where management was stopped for economic reasons. Since 1996, traditional, extensive grassland management has been re-established in the area of 18 ha (Manhart *et al.* 2003) as a re-

Table 1. Characteristics of sample plots and the scheme of mowing applied in plots during the restoration period. Number of cuts per year and their approximate terms are given.

Plot (ha)	Soil type ¹⁾	Humidity in 2004 ²⁾	Vegetation classification in 1995	Usage before 1995 ³⁾	Usage in 1996–2000	Usage in 2001 to 2005
A1 (0.8)	Floodplain gley/fen (Lu)	wet	<i>Arrhenatherion</i> (eutrophic)	A	3 cuts: June, Aug and Sep	1 cut: mid June–mid Oct
A2 (0.6)	Floodplain gley/wet gley (Lu)	fresh	<i>Arrhenatherion</i> (eutrophic)	A	2 cuts: late June, late Oct	1 cut: mid June–mid Oct
A3 (0.2)	Gley-pseudogley (uL)	fresh	<i>Arrhenatherion</i>	A	2 cuts: early June, late Aug	2 cuts: late May, early Oct
C1 (1.7)	Floodplain gley/wet gley (Ut4/Lu)	wet	<i>Calthion</i> (species-poor)	A	2 cuts: late July – early Aug, mid Sep– early Oct	
C2 (0.6)	Floodplain gley/wet gley (Lu)	wet	<i>Calthion</i> (sedges-formation)	A	2 cuts: mid June–mid July; mid Sep–early Oct	
C3 (0.7)	Brown soil/para brown earth (Ut4/Tu4)	moderate dry	<i>Calthion</i> (species-poor)	A	1–4 cuts: mid June, further cuts: irregularly	
C4 (0.7)	Floodplain gley/wet gley (Ut4)	fresh	<i>Calthion</i> (sedges-formation)	A	2 cuts: late July, mid Oct	2 cuts: mid June, mid Sep
C5 (0.6)	Floodplain gley/wet gley (huL)	fresh	<i>Calthion</i> (sedges-formation)	A	2 cuts: late July, mid Sep–mid Oct	
INT (4.9)	Fen (uL)	wet	Intensively farmed meadow	A	5 cuts for silage; fertilization with liquid manure	
EXT (several)	Fen (Heavy decomposed fen-peat)	semi-wet	Extensively farmed <i>Molinion/Calthion</i>	B	1 autumn cut for litter	

¹ Abbreviations: h – humous, s – sandy, u – silty, t – clayey, U – silt, L – clay, Ut4 – very muddy silt, Tu4 – very silty clay.

² The classification of degrees of moisture was conducted according to Succow and Joosten (2001)

³ A – up to 5 cuts, mineral fertilization, liquid manure, grazing afterwards, B – mown for litter, once a year, in Autumn.

sult of complete cessation of fertilization and a decreasing number of cuts (to 2 per year). At the end of study period *Cirsium oleraceum* (cabbage thistle) meadows, *Arrhenatherum* (false oat-grass) meadows, *Molinia* (purple moor-grass) meadows, as well as tall-herb communities (of the alliance *Filipendulion*) are the dominant vegetation types in that area. As a reference, unchanged plot, extensively managed grassland was also sampled, located in the wetland and peat-bog complex of Schönramer Filz (see Ehmer-Künkele 1983), 500 m north-north-west of the village Moosen (6 km south from the complex of above described, experimental plots).

MATERIAL AND METHODS

Experimental plots

Although the study covered broad spectrum of various habitats, representing mosaics of vegetation cover occurring in the area, for controlling the effect of habitat variability on insect community, in the paper we focus on only two kinds of common grasslands – *Calthion* (five plots: C1–C5) and *Arrhenatherion* (three plots: A1–A3). The plots (0.2–1.7 ha) were distributed in a part of the valley at the length of 800 m and most of them were adjoining to each others or distance between them amounted to several ten meters. Besides the experimental plots, the insects were sampled also in two reference plots, managed in unchanged way for a long time, including the study period. The first one was an intensively managed meadow (called INT here), adjacent to experimental plots, and the second one (mentioned above in “Study area”) was an extensive meadow (called EXT), for decades mown for litter only in autumn. The latter plot contained mainly patches of *Molinia* meadows, fen (*Caricion davallianae* and *Caricion fuscae*) and peat-bog vegetation in a small-scale mosaic (Table 1).

Management of the sampled areas during the restoration period

Basic treatments that have been applied to restore grasslands were cessation of fertilization and a reduction of number of cuts per year (Table 1). The plots were harrowed in

spring (usually in March) and vegetation was mowed once or twice a year by a rotary mower at height of 5–10 cm. The cut material was removed. In some cases they were cut more frequently. The first cut was done between late May and late August, depending on the state of vegetation and the weather. To reduce the production of plant biomass, the frequency of mowing decreased to 1–2 per year in 2001–2005 (Table 1). Such treatment led to decrease in fertility and increase in humidity of the habitat in the study area as indicated by the Ellenberg values N and F, respectively (Sachtleben *et al.* 2007).

Insect survey

The suction trap powered by a generator (Ryszkowski and Karg 1977) with sampled area of 0.25 m² was used during the study period. Ten sub-samples were taken from each plot once or twice a year (June–August), in 10 places (i.e. one sub-sample in one place) that were distributed more or less evenly along randomly established transect across a given plot. Specimen were identified to genus or family level and dried. Number of families was used as an index of insect diversity. It is worth mentioning that according to Baldi (2003), the number of families (total per plot per year) may be considered reliably as a surrogate of species number in grasslands, useful for making comparison in space or time.

Ten sub-samples taken from a given plot were pooled as one sample and used in further analyses. On the basis of identification guides by Kratochvil (1957, 1959) and many issues of the serie “Keys for the identification of Polish Insects” published by the Polish Entomological Society, the insects were divided into four trophic groups: phytophages, saprophages, predators and parasites (Appendix 1). The classification of insects into trophic groups is difficult due to complexity of insect feeding ecology, as well as some gaps in knowledge on feeding habits of many species. In case of some families (mostly from the orders Diptera and Hymenoptera) there was necessary to classify them arbitrarily into a given trophic group. It was despite the possibility of appearance of species belonging to a different trophic group or against the contradictory data on feeding ecology of given taxa, contained in some ref-

erences. In case of families with mixed trophic, they were assigned to one of the groups mentioned above on the basis of prevailing trophic according to genus level. In case of species where adults (imagines) feed on flower nectar or do not feed at all, the basis for the classification was feeding ecology of larvae.

Datasets and statistics

Changes in the insect community were analysed in two datasets: (1) short-term comparison in space (2004–2005), i.e. between eight restored (A1–A3, C1–C5) and two reference, intensively (INT) and extensively (EXT) cultivated plots sampled twice a year (in June and August); (2) long-term comparison between five restored plots (A2, A3, C1–C3) in time. The study was carried out 3–4 years before restoration (1992–1993) and 1–9 years after the restoration start (1997, 1998, 1999, 2000, 2004 and 2005). The plots were sampled 1–2 times per year in June–August, but only one sample taken in June (in most cases) was taken to analyse the data as much comparable as possible.

The following statistical tests and procedures were used:

a) Mann-Whitney *U* test – for variables with abnormal distribution, to assess whether two samples of observations have equally large values;

b) t-test for single sample – for comparison between restored and reference plots;

c) General Linear Model (GLM) for assessing the effect of a year, a period and a plot on insect abundance and number of families (years nested in period, fixed effects – period and year, random effect – plot);

d) Morisita's index (by Hammer *et al.* 2008) was used to assess similarity of taxonomic composition between years and between plots;

e) coefficient of variability (SD/arithmetic mean) was used as a measure of variability of family number between plots (proxy for beta-diversity);

f) evenness of community trophic structure was quantified with the aid of evenness index *J'* (Pielou 1966).

All the tests and estimations were performed with the aid of Statistica 7.1 and PAST 1.86b (Hammer *et al.* 2001).

RESULTS

Short-term (2004–2005) comparison of restored and reference plots

As the differences in both insect density and number of families between *Arrhenatherion* and *Calthion* sample plots were statistically insignificant ($P > 0.2$ in Mann-Whitney test for both variables and for each of all four dates), the data from these grassland types were pooled and considered jointly as data from restored plots.

The mean insect abundance in restored plots in 2004–2005 amounted to 94.0 ± 34.8 ind m^{-2} and was on average higher than in the INT reference plot – 73.9 ± 39.7 ind m^{-2} , and lower than in the EXT reference plot – 106.6 ± 47.7 ind m^{-2} . The data for single dates matched this averaged pattern. In three out of four dates the density of insects in restored plots was higher than in the INT reference plot. However, the differences were statistically insignificant or marginally significant (Table 2). The exceptional circumstances were met in August 2005, when the density in the INT plot was very high because of extremely numerous occurrence of Iassidae (*c.* 30 ind m^{-2}), which contributed to higher total density in the INT reference plot. At the same time, the insect density in restored plots tended to be lower (three out of four dates, but only one difference was statistically significant) than in the EXT reference plot (Table 2).

The pattern of differences in the number of families was much more consistent. Average number of families per plot per date (36.4 ± 5.9) was between the number found in the INT (29 ± 3.9) and the EXT (47.5 ± 5.3) reference plots. The pattern was the same also for all individual dates (Table 2). Seven out of eight differences were statistically significant and one was close to significant. The values observed in restored plots were on average closer to the values in the INT reference plot than in the EXT reference plot (in seven of eight cases).

The pattern of the differences in insect density between restored and reference plots differed among trophic guilds (Fig. 1). In case of saprophages, the detection of trends was

Table 2. Mean total insect abundance (ind m⁻²) and mean total number of families in restored (mean per plot) and reference (managed intensively and extensively) plots with statistical significance (t-test for single sample). The confidence interval (95% CI) for intensively and extensively managed grasslands is not given as they were represented by single plots. The bold values indicate a significant effect.

Parameter	Restored plots (mean±95%CI)	Reference plot		Statistical significance of differences					
		Intensive	Extensive	Restored vs. Intensive			Restored vs. Extensive		
				t	df	P	t	df	P
Abundance									
Jun 2004	97.5±51.8	58.4	70.0	1.78	7	0.1175	1.25	7	0.2499
Aug 2004	122.1±38.5	80.8	133.6	2.54	7	0.0389	-0.71	7	0.5036
Jun 2005	70.1±20.8	50.4	94.4	2.22	7	0.0614	-2.76	7	0.0282
Aug 2005	86.2±26.4	106.0	128.4	-1.77	7	0.1194	-3.78	7	0.0069
Number of families									
Jun 2004	33.1±4.9	28.0	47.0	2.49	7	0.0414	-6.75	7	0.0003
Aug 2004	40.6±4.9	33.0	53.0	3.72	7	0.0075	-6.03	7	0.0005
Jun 2005	33.4±7.8	26.0	43.0	2.22	7	0.0618	-2.90	7	0.0230
Aug 2005	38.4±3.8	31.0	50.0	4.54	7	0.0026	-7.15	7	0.0002
Mean	36.4	29.0	47.5						

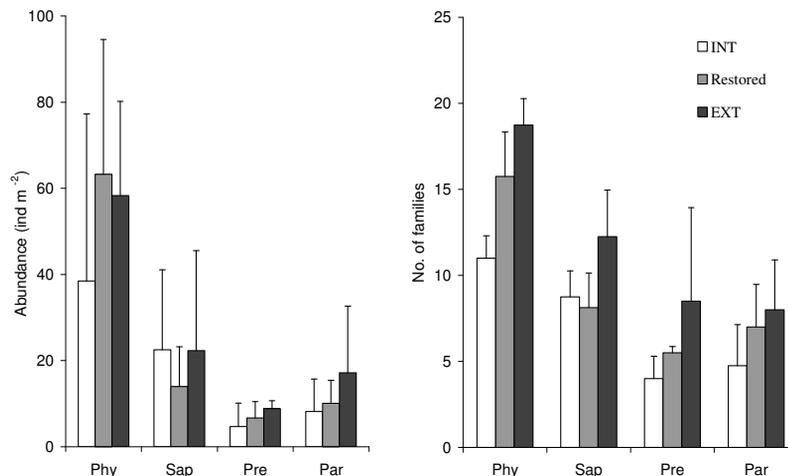


Fig. 1. Insect abundance (ind m⁻²) and number of families in trophic guilds (means for four dates in 2004–2005, with 95% CI) in restored and reference (INT and EXT) plots. INT – meadow managed intensively, EXT – meadow managed extensively, Phy – phytophages, Sap – Saprophages, Pre – predators, Par – parasites.

impossible as the direction of the differences between the INT and the EXT reference plots changed from date to date (Table 3), and their means were equal. Generally, the abundance of saprophagous insects in restored plots tended to be lower than in both INT and EXT reference plots (Fig. 1). The results suggest that insect density in that guild was not related to the mode of meadow cultivation. Mean density of phytophagous insects in restored plots was on average higher than in the INT reference plots and close to the EXT ref-

erence plot (Fig. 1), but the direction of differences changed from date to date (Table 3), thus the impact of cultivation intensity on phytophages is unclear. For both predatory and parasitic insects, their abundance was intermediate on average (Fig. 1); however, the difference between the EXT and restored plots was on average larger and more significant than the difference between restored and the INT reference plots (Table 3).

The pattern of differences in the number of families in trophic guilds was more con-

sistent. Both on average (Fig. 1) and in single dates (Table 4), mean number of families in individual trophic guilds was between the INT and the EXT reference plot, apart from saprophages whose number of families was close to that in the INT reference plot and clearly lower than in the EXT reference plot (Fig. 1 and Table 4). Many of the differences were statistically significant (Table 4).

Long-term (1992–2005) changes in insect communities during restoration

Changes in abundance and taxonomic richness

The mean density of epigeic insects in five sampled restored plots in 1992–2005 varied

from 37 to 135 ind m⁻², mean number of families – from 25 to 42, and total number of families – from 52 to 81. A peak of taxonomic richness (both mean and total number of families) occurred in 1998 and after that the number of families tended to decline up to level slightly higher than averaged level observed before restoration start (Fig. 2). It may be concluded that 1998–2000 were the years with highest level of both taxonomic richness and abundance. The mean number of families amounted to 73.7 in that period while in other years after restoration start (1997, 2004 and 2005) it was equal to 57.3. Among seventeen families found in 1998–2000 but not in 1997, 2004 and 2005 were: Argidae, Athribidae, Buprestidae, Chrysopidae, Cicadellidae, Dryopidae, Fungivoridae, Gracillaridae, Hesperidae, Lachesillidae,

Table 3. Mean insect abundance (ind m⁻²) in trophic guilds in restored and reference (managed intensively and extensively) plots, with statistical significance (t-test for single sample). The confidence interval (95% CI) for intensively and extensively managed grasslands is not given as they were represented by single plots. The bold values indicate a significant effect.

Trophic guild	Restored plots (mean±95%CI)	Reference plot		Statistical significance of differences					
		Intensive	Extensive	Restored vs. Intensive			Restored vs. Extensive		
				t	df	P	t	df	P
Saprophages									
Jun 2004	9.0±3.2	32.0	12.4	-16.93	7	0.0000	-2.50	7	0.0408
Aug 2004	22.3±9.2	32.4	44.0	-2.58	7	0.0362	-5.56	7	0.0008
Jun 2005	11.8±4.6	8.8	17.2	1.55	7	0.1658	-2.78	7	0.0271
Aug 2005	12.7±4.0	16.8	15.6	-2.43	7	0.0452	-1.72	7	0.1289
Mean	14.0	22.5	22.3						
Phytophages									
Jun 2004	74.0±48.4	16.8	42.4	2.79	7	0.0269	1.54	7	0.1672
Aug 2004	84.9±48.2	35.6	60.4	2.42	7	0.0462	1.20	7	0.2687
Jun 2005	41.6±11.3	28.4	54.8	2.76	7	0.0280	-2.78	7	0.0271
Aug 2005	52.8±19.5	73.2	75.6	-2.49	7	0.0418	-2.78	7	0.0274
Mean	63.3	38.5	58.3						
Predators									
Jun 2004	4.9±2.6	4.4	8.8	0.45	7	0.6682	-3.49	7	0.0102
Aug 2004	5.5±3.2	2.8	10.4	2.01	7	0.0843	-3.69	7	0.0077
Jun 2005	10.2±6.8	9.6	8.4	0.21	7	0.8412	0.62	7	0.5525
Aug 2005	6.2±3.8	2.0	7.6	2.58	7	0.0367	-0.90	7	0.3990
Mean	6.7	4.7	8.8						
Parasites									
Jun 2004	9.6±4.7	5.2	6.4	2.22	7	0.0617	1.62	7	0.1501
Aug 2004	9.4±4.3	10.0	18.8	-0.32	7	0.7577	-5.22	7	0.0012
Jun 2005	6.5±3.3	3.6	14.0	2.06	7	0.0783	-5.33	7	0.0011
Aug 2005	14.7±3.9	14.0	29.6	0.40	7	0.7025	-9.15	7	0.0000
Mean	10.0	8.2	17.2						

Table 4. Mean number of families in trophic guilds (per plot) in restored and reference (managed intensively and extensively) plots, with statistical significance (t-test for single sample). The confidence interval (95%CI) for intensively and extensively managed grasslands is not given as they were represented by single plots. The bold values indicate significant differences.

Trophic guild	Restored plots (mean±95%CI)	Reference plots		Statistical significance of differences					
		Intensive	Extensive	Restored vs. Intensive			Restored vs. Extensive		
				t	df	P	t	df	P
Saprophages									
Jun 2004	6.2±1.2	8.0	12.0	-3.33	7	0.0127	-10.93	7	0.0000
Aug 2004	9.0±1.3	10.0	13.0	-1.76	7	0.1211	-7.06	7	0.0002
Jun 2005	8.7±2.2	8.0	14.0	0.81	7	0.4423	-5.70	7	0.0007
Aug 2005	8.5±2.0	9.0	10.0	-0.59	7	0.5727	-1.77	7	0.1192
Mean	8.1	8.7	12.2						
Phytophages									
Jun 2004	15.3±1.3	11.0	19.0	7.60	7	0.0001	-6.71	7	0.0003
Aug 2004	17.8±2.6	10.0	20.0	7.06	7	0.0002	-2.05	7	0.0796
Jun 2005	13.9±2.7	11.0	18.0	2.56	7	0.0378	-3.67	7	0.0080
Aug 2005	16.1±1.5	12.0	18.0	6.45	7	0.0003	-2.93	7	0.0219
Mean	15.5	11.0	18.7						
Predators									
Jun 2004	5.6±2.6	3.0	9.0	2.42	7	0.0461	-3.11	7	0.0170
Aug 2004	5.4±1.5	5.0	7.0	0.60	7	0.5674	-2.60	7	0.0354
Jun 2005	5.3±2.0	4.0	5.0	1.45	7	0.1898	0.29	7	0.7799
Aug 2005	5.8±1.9	4.0	13.0	2.20	7	0.0639	-9.11	7	0.0000
Mean	5.5	4	8.5						
Parasites									
Jun 2004	6.0±1.3	4.0	7.0	3.74	7	0.0072	-1.87	7	0.1036
Aug 2004	8.6±1.7	6.0	10.0	3.72	7	0.0074	-1.95	7	0.0923
Jun 2005	5.4±2.1	3.0	6.0	2.68	7	0.0314	-0.71	7	0.5029
Aug 2005	8.0±1.0	6.0	9.0	4.73	7	0.0021	-2.37	7	0.0499
Mean	7.0	4.7	8.0						

Liviidae, Plutellidae, Psychodidae, Sarcophagidae, Satyridae, Tortricidae, Torymidae. The set of these families includes species with various biological traits and there is no common feature for all or most of these taxa that could be helpful at explaining their occurrence only in that period.

According to applied GLM mixed model, the total insect abundance after conversion was on average significantly higher than before (i.e. effect of period has been proved) and no interaction between effect of period and plot was found (Table 5). Thus, the averaged increase of insect abundance after conversion was consistent among all restored plots (Fig. 3). The effect of a year was much less important, and the effect of a plot was insignificant. Similar pattern was valid also for the

mean number of families (Table 5, Fig. 3). It was much higher after conversion than before, while the effect of a year and a plot was insignificant.

Changes in trophic structure

The trophic structure has been changing from year to year; however, no trend and no difference in both average proportions and evenness (J') between periods before and after conversion were found (Fig. 4). The most distinct was the increase in the mean share of predatory species, but both in terms of density (from 7.4 to 11.7%) and number of families (from 12.6 to 17%) the increase was statistically insignificant ($P=0.53$ and $P=0.97$ in Chi-square test, respectively).

Table 5. One-dimensional significance test of effect of period ('before' – 1992–1993, 'after' – 1997–2005), year (single one) and plot on total insect abundance and the number of families in GLM ('year' nested in 'period'). The bold values indicate a significant effect.

Variable	Effect	df	MS	F	P
Abundance					
Constant	Fixed	1	197977.4	303.7	0.0005
Period	Fixed	1	13593.7	30.1	0.0054
Year (Period)	Fixed	6	2372.5	2.4	0.0584
Plot	Random	4	690.7	1.5	0.3458
Period × Plot	Random	4	452.2	0.5	0.7659
Error		24	988.2		
Number of families					
Constant	Fixed	1	36648.0	1038.7	0.00008
Period	Fixed	1	1068.0	32.1	0.00478
Year (Period)	Fixed	6	114.7	2.2	0.08196
Plot	Random	4	37.2	1.1	0.45773
Period × Plot	Random	4	33.2	0.6	0.64663
Error		24	52.9		

Table 6. Similarity of insect assemblages (mean values of each-to-each comparisons made with the use of Morisita's index) and variation in the number of insect families (CV) between the plots A2, A3, C1, C2, C3 in 1992–2005.

Year	Mean Morisita's similarity index	Variation (CV) of family number
Before conversion		
1992	0.71	0.30
1993	0.55	0.12
After conversion		
1997	0.82	0.08
1998	0.84	0.07
1999	0.64	0.15
2000	0.53	0.14
2004	0.52	0.17
2005	0.58	0.32

Changes in taxonomic composition structure

The value of Morisita's similarity index used for comparison between 1992 and 1993 amounted to 0.64, while mean value of that index for comparison between 1992 and the years 1997–2006 was equal to 0.73 ± 0.08 (95% CI), and between 1993 and the years 1997–2006 was equal to 0.63 ± 0.05 (95% CI). The year-to-year similarities (Morisita's index) in 1997–2005 amounted to: 0.55, 0.95, 0.91, 0.71, 0.87 and 0.79, respectively. All these analyses (together with no trends in the change in the number of families) indicate that the changes in taxonomic composition (as reflected by list

of species and their abundance) could be described as fluctuation rather, but not a consistent trend.

Changes in spatial diversity of insect community richness

No clear pattern of changes in composition of insect assemblages was found. Both mean similarity of sampled plots (assessed by Morisita's index) and variation of taxonomic diversity changed irregularly (Table 6). Relatively high value of Morisita's index and low coefficient of variability of number of families suggest that the insect assemblages of sam-

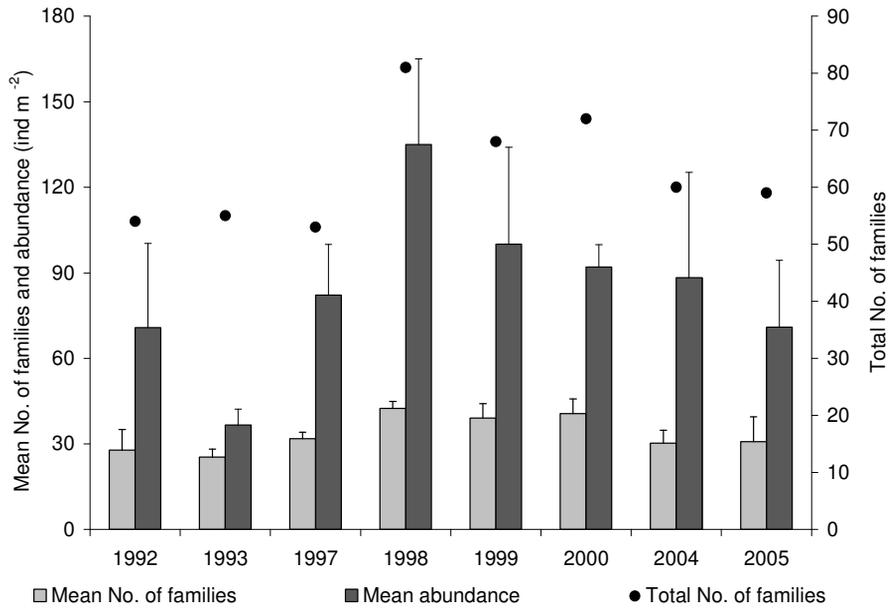


Fig. 2. Insect abundance (ind m⁻², means with 95% CI) and taxonomic richness (number of families per plot) in restored plots (N = 5) in the years before (1992–1993) and after (1997–2005) conversion.

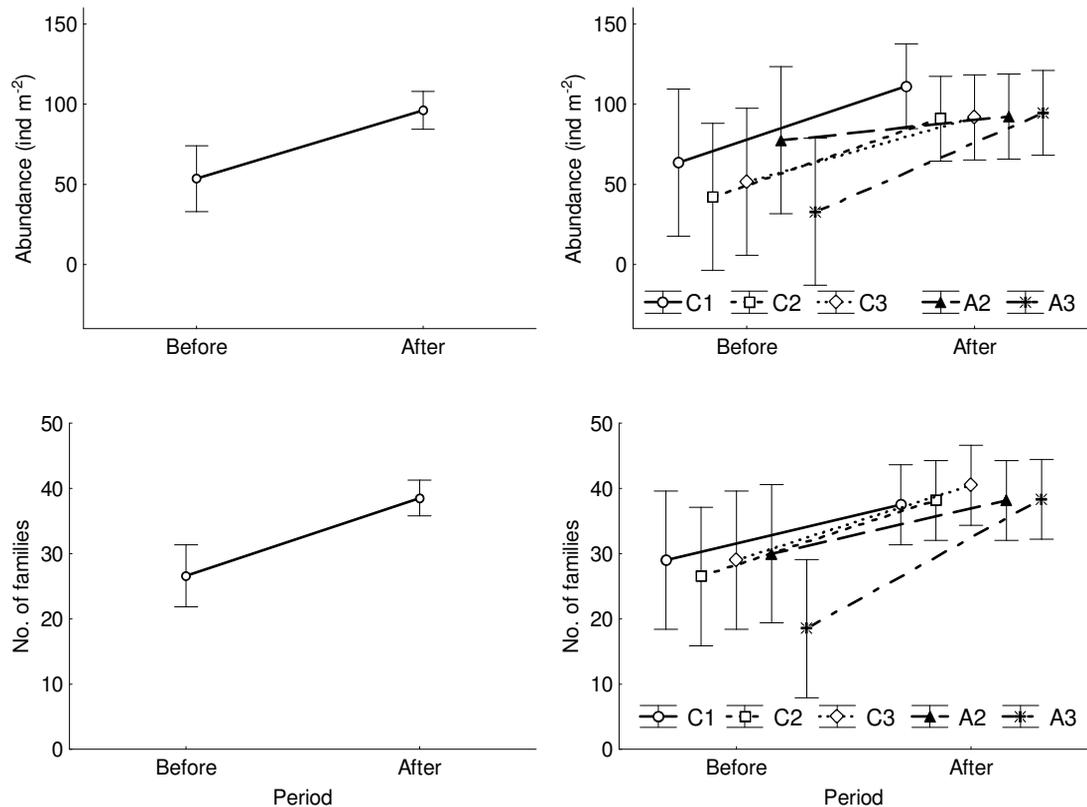


Fig. 3. Mean insect abundance (ind m⁻²) before (1992–1993) and after (1997–2005) conversion (left) and interactions (right) between total abundance and periods and sample plots (A2, ..., C3) – expected values with 95% CI estimated with the use of GLM (see Table 5) are given.

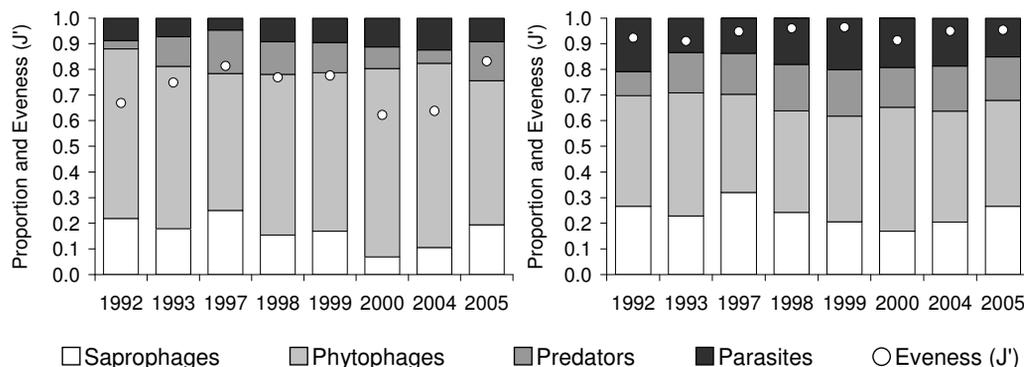


Fig. 4. Trophic structure (proportions and Evenness index J') of epigeic insect community in the restored plots ($n = 5$) in the years before (1992–1993) and after (1997–2005) conversion, with respect to insect abundance (left) and number of families (right).

pled plots were most similar to each other in 1997–1998. After that, the variation of number of families increased up to $CV = 0.32$, however similarity of taxonomic composition between the plots remained at the level (0.52–0.64) observed before (0.55–0.71) start of restoration, contrary to expectations, that spatial diversity of insect communities should increase as a result of extensive management.

DISCUSSION

The analyses presented here show that insect response to restoration treatment was unclear and slow, on average, in particular when long-term trends are considered. In short-term survey, after 8–9 years after the beginning of restoration, the mean insect abundance and number of families in restored plots were slightly higher than in intensively managed meadow (and at the same time markedly lower than in extensively managed one for many years). In the analysis of long-term monitoring data (1992–2005), both insect abundance and diversity were on average higher during restoration period than before. The peaks of both number of families and insect abundance were recorded in the years 1998–2000, but in the next five years a decrease was observed, up to values close to observed before restoration. The lack of clear response of insect community was reflected also by analysis of taxonomic similarity. One could expect that the difference in insect community between initial (before restoration) and current (after

restoration) status increases in time, due to arriving of new taxa, including rare, stenotopic ones. However, no such trend was found. In particular, the pair-wise similarity between a year before and successive years after restoration start did not decrease, as it could be expected as a result of the coming of new taxa.

The peak of abundance and taxonomic richness in 1998–2000 can be related to some changes in vegetation in sample plots, quantified by Sachtleben *et al.* (2007) with the use of the Ellenberg values (L – light, F – moisture and N – fertility). The maximum of L and F (indicating the best conditions for photophilous and hygrophilous species), and minimum of N value (best conditions for plant species that prefer low soil fertility) was observed just in 2000, namely in period (1998–2000) when the insect abundance and richness reached the highest number. However, the reason for such coincidence is unclear.

The results on response of insects at community level are in line with the conclusions from earlier studies. For example, Woodcock *et al.* (2012) reported about “lag” between restoration and the establishment of phytophagous beetle assemblages and claimed that the success in insect restoration would plateau after 20 years, representing *c.* 60% increase in assemblage similarity to target grasslands. However, it should be underlined that in that case restoration treatment included seed addition and in the experimental plots, where no seeds were added, the similarity to the target grasslands did not increase over time. Similarly, Hemerik

and Brussaard (2002) showed no relation of ground beetle (as well as all studied macro-invertebrates) taxonomic composition with successional stage of restored grassland when plots not fertilized during 7, 11, 24 and 29 years were compared. Woodcock *et al.* (2008) studied restoration success of plant and phytophagous beetle assemblages in restored species-rich mesotrophic grasslands and concluded that “*it is possible that the long-term consequences of the management treatments would not be establishment of beetle and plant community characteristic of the targets of the restoration.*” The authors also proved that hay spreading (as a source of target plant species seeds), and some dedicated soil disturbance techniques can increase community similarity in both plants and insects to that of species-rich grasslands and thus raise conservation value of such restored grasslands.

The reasons for such pattern of rather weak and slow response of insect communities to restoration treatment are poorly recognized. Presumably, some causes listed and explained by Woodcock and McDonald (2010) with respect to restoration of species-rich flood-plain grazed meadows may play important role also in other grassland types. They are as follows:

1) In many cases restoration treatment covers target plant species seed addition, whereas insect colonisation of restored areas is by natural immigration. Thus, similarity of restored grasslands to the target ones may be at least partially artificial and not observed for other trophic levels.

2) Unfavourable landscape structure. Lack of “source” habitat for some species in neighbourhood of restored grasslands may be a basic limiting factor for insect restoration success (as in meta-population dynamic model). It was found that for some species even relatively small amount (and thus distance to pass) of unfavourable habitat may provide a barrier to stop or strongly decline rate of colonization (Wratten *et al.* 2003) and from the other hand, connectivity between restored grasslands may strongly diversify the colonisation success of animal taxa depending on their dispersal abilities (Knop *et al.* 2011).

3) Competition between rare and common insect species. A restored grassland may be immediately colonised by common

and abundant species of insects that could be classified as generalists and having small conservation importance. These species can compete with other ones (rare, more specialized species) that can stop desired and expected increase in taxonomic richness and in similarity to target habitat. It could result in establishment of a stable state, alternative to that expected (Hirst *et al.* 2005).

Because of strongly heterogenic structure of the study area, composed of small habitat patches, it seems the rate of immigration to restored areas should be high, so most probable factor responsible for slow response of insect communities is an interspecies competition leading to establishment of an alternative stable state characterized by unexpectedly low increase in taxonomic richness.

Another explanation of slow and little changes in insect community recorded in studied sample plots, not mentioned in the paper cited above (Woodcock and McDonald 2010), is high mobility of most insects, both with the aid of wings and legs. High ability to move from one patch to another, with connection to small distances between the patches, could “diffuse” positive effect of restoration to adjacent not restored places as it was shown by Albrecht *et al.* (2010) for Swiss grasslands. In result, increase in taxonomic richness and insect abundance in restored places may be limited by permanent emigration and day-to-day insect movement.

Even considering the trophic structure, the results of restoration are ambiguous. As Albrecht *et al.* (2007) show, the restoration of grassland can significantly affect trophic structure, leading to e.g. higher species richness of particular trophic level, linkage diversity and interaction diversity. In the study presented here, short-term comparison suggests positive response of phytophagous, predatory and parasitic insects in terms of abundance and number of families (much more clear in the second variable), however long-term analysis show year-to-year fluctuations in proportion to particular trophic guilds, with no increase in the share of any trophic guild.

Again, from these fluctuations it may be concluded that high movement ability of many insect taxa can disturb and mask the pattern that could describe response of insect

communities to restoration effect. That assumption could also explain why taxonomic similarity between the restored plots did not decrease, in particular when taking into account the spatio-temporal insect interactions between these sample plots. The other factor that could be responsible for year-to-year non-directional changes is weather conditions.

It is also worth highlighting that although the analyses performed at the family level do not enable to explain species-related changes in entomofauna, they seem to be adequate for describing general processes in an insect community. The usefulness of the number of families as a proxy for species richness has been confirmed in Hungarian grasslands on basis of large number of samples (Baldi 2003). From the other side, classification of some families to given trophic (homogenous) group can be considered as controversial, however the number of such families (they are, e.g. Dolichopodidae, Cecidomyiidae, Bibionidae) is low, and the share of their representatives in the community is small.

CONCLUSIONS

The changes in the insect community recorded in 14-year study support findings from other studies which revealed that response of insect community to restoration treatment is rather slow when averaged trends are considered. When the increase in taxonomic diversity and abundance of insects is the target of restoration, the changes in insect community described in the paper have to be assessed as slow, on average (despite some fluctuations that appeared in our study). The short-term (two-year) comparison between restored and reference plots, eight years after start of restoration, shows that the first ones had supported more diverse (in term of family number) insect communities as a whole, as well as in guilds of predatory and parasitic species. However, long-term trend analysis shows that since 1998–2000 insect diversity and abundance has been declining. Thus, long-term monitoring revealed a far more complex picture of the responses and patterns than short term surveys. No clear trend both in total insect abundance and taxonomic richness was

detected during studied period as it could be expected during conversion of grassland from intensively into extensively managed one. Also trophic structure fluctuated without defined trend.

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Appendix 1. Insect families found in the study and their classification to trophic groups (accepted in the paper). L – larvae, pa – parasites, ph – phytophages, pr – predators, sa – saprophages.

Acridiidae	ph	Dryinidae	pa	Pentatomidae	ph
Acridiidae (L)	ph	Dryopidae	sa	Pentatomidae (L)	ph
Agrionidae	pr	Elateridae	ph	Phalacridae	sa
Agromyzidae	ph	Empididae	pr	Phoridae	sa
Anthocoridae	pr	Encyrtidae	pa	Piesmidae	ph
Anthomyiidae	ph	Ephydriidae	pr	Piesmidae (L)	ph
Anthribidae	sa	Eriocraniidae	ph	Pipunculidae	pr
Aphelinidae	pa	Eucoilidae	pa	Plutellidae	ph
Apidae	ph	Eulophidae	pa	Pompilidae	pr
Argidae	ph	Eumenidae	pr	Proctotrupidae	pa
Asilidae	pr	Eurytomidae	ph	Pselaphidae	sa
Asteidae	sa	Fungivoridae	sa	Psychodidae	sa
Bibionidae	sa	Geometridae	ph	Pteromalidae	pa
Blattidae	sa	Gracillariidae	ph	Pyralidae	ph
Braconidae	pa	Gryllidae (L)	ph	Rhagionidae	pr
Bruchidae	ph	Heleidae	pr	Saldidae	sa
Buprestidae	ph	Helodidae	ph	Sarcophagidae	sa
Calliphoridae	sa	Hemerobiidae	pr	Satyridae	ph
Cantharidae	pr	Hesperidae	ph	Scatophagidae	sa
Cantharidae (L)	pr	Heteroptera (L)	ph	Scatopsidae	sa
Carabidae	pr	Hydrophilidae	sa	Scelionidae	pa
Carabidae (L)	pr	Iassidae	ph	Sciaridae	sa
Cecidomyiidae	ph	Iassidae (L)	ph	Sciomyzidae	pr
Cerambycidae	ph	Ichneumonidae	pa	Sepsidae	sa
Ceraphronidae	pa	Lachesillidae	sa	Simuliidae	sa
Cercopidae	ph	Lampyridae (L)	pr	Sphaecidae	pr
Cercopidae (L)	ph	Lathridiidae	sa	Sphaeroceridae	sa
Chironomidae	sa	Lauxaniidae	sa	Staphylinidae	sa
Chloropidae	ph	Lepidoptera (L)	ph	Staphylinidae (L)	sa
Chrysomelidae	ph	Limoniidae	sa	Stratiomyidae	sa
Chrysomelidae (L)	ph	Liviidae	ph	Syrphidae	pr
Chrysopidae	pr	Lonchaeidae	sa	Tabanidae	sa
Chrysopidae (L)	pr	Lygaeidae	ph	Tachinidae	pa
Cicadellidae	ph	Lygaeidae (L)	ph	Tenthredinidae	ph

Cixiidae	ph	Malachiidae	pr	Tenthredinidae (L)	ph
Clambidae	sa	Micropezidae	ph	Tephrytidae	ph
Coccinellidae	pr	Milichiidae	sa	Tetrigidae	ph
Coccinellidae (L)	pr	Miridae	ph	Tettigoniidae	ph
Coleoptera (L)	ph	Miridae (L)	ph	Tettigoniidae (L)	ph
Coreidae	ph	Muscidae	ph	Tingidae	ph
Coreidae (L)	ph	Musidoridae	sa	Tingidae (L)	ph
Cryptophagidae	sa	Mymaridae	pa	Tipulidae	sa
Culicidae	sa	Myrmicidae	pr	Tortricidae	ph
Curculionidae	ph	Nabidae	pr	Torymidae	pa
Cynipidae	ph	Nabidae (L)	pr	Trichoceridae	sa
Cypselidae	sa	Nitidulidae	ph	Trichogrammidae	pa
Dasytidae	ph	Noctuidae	ph	Trichoptera	sa
Delphacidae	ph	Nymphalidae	ph	Triozidae	ph
Delphacidae (L)	ph	Oedemeridae	ph	Trypetidae	ph
Diapriidae	pa	Opomyzidae	ph	Vespidae	pr
Dolichopodidae	pr	Pamphiliidae	ph	Zygaenidae	ph
Drosophilidae	sa	Panorpidae	pr		
