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Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure

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Summary

1. During the last few years a variety of methods have been applied in Switzerland to preserve and enhance biological diversity in agricultural systems. The purpose of this study was to evaluate grassland management techniques in respect of their effectiveness within a managed area and to examine how these areas contribute to species diversity at a landscape scale.

2. We examined insect diversity in grasslands subject to different management in a heterogeneous landscape in part of the Swiss Jura. Four study areas with varying landscape structure were selected and, in each area, meadows of two grassland management types were investigated.

3. The true bugs (Heteroptera) were chosen as an indicator group for insect diversity on the basis of previous work that had shown that the richness of the bug fauna correlates strongly with total insect diversity.

4. The variance of the heteropteran species data was partitioned into spatial (area) and management components. Area accounted for 35·4%, management for 29·7% and the interaction management × area for 7·2% of the species variance. The species diversity was greater in extensively managed meadows than in intensive ones; extensive sites had more individuals and showed a more even rank abundance distribution.

5. Individual species differed in their responses to management. Two species benefited from intensification whereas six species were affected negatively by intensive management. Two main groups of species did not appear to respond to management; these were mostly widespread species occurring in a variety of habitats, and polyphagous species which live in a wide range of grasslands but which show a certain affinity to managed meadows.

6. Our study indicates that extensive management of grasslands can enhance both local and regional insect diversity in agricultural landscapes. Extensively managed meadows were species-rich habitats that supported some rare and specialized species. In contrast, the bug community of intensive meadows was dominated by more widespread and less specialist species.

Key-words: grassland management, Heteroptera, regional diversity, species diversity, Switzerland.

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Introduction

Agricultural landscapes are characterized by a very high spatial and temporal heterogeneity determined largely by human activities. Little is known about how species are affected by such heterogeneity and how they persist in agricultural systems (Macdonald & Smith 1990). For example, few studies have investigated the dispersal and dispersion of arthropods in agricultural landscapes (Samways 1994; Forman 1995; Mortimer, Hollier & Brown 1998) although there is information on some groups, notably butterflies (Fry 1994; Sutcliffe & Thomas 1996), spiders (Bishop & Riechert 1990; Thomas, Hol & Everts 1990; Thomas 1996), carabid beetles (Thomas, Wratten & Sotherton 1991; Kinnunen & Tiainen 1994; Forman 1995) and wild bees (Steffan-Dewenter 1998).

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In contrast, there have been several studies of the influence of grassland management on insect diversity; for an overview see Curry (1994) and Gerstmeier & Lang (1996). Some management operations, for example mowing, have a direct effect on insects by damaging or killing individuals or removing them from the site. Immobile and relatively immobile species or life-cycle stages are specially affected, and in the long term the whole population may be threatened (Völkl *et al.* 1993). Indirect effects may also occur through changes to the habitat; for example, if management alters the plant species composition and the structure of the vegetation, it is also likely to affect the microclimate and other aspects of the microhabitat. Because many arthropods are very sensitive to microclimatic conditions, such indirect effects may alter community composition (Franz 1931; Fewkes 1961; Curry 1994; Gerstmeier & Lang 1996; Painter 1999). Leafhoppers (Auchenorrhyncha) are known to be strongly affected by indirect effects of grassland management. They are closely associated with particular plant species and reach their greatest diversity in species-rich highly structured meadows. Many species occupy definite layers in a grassland and move vertically within the sward during the season. Changes in the species composition and structure of the plant community due to management will therefore affect leafhoppers greatly (Andrzejewska 1965; Curry 1994).

Although it is recognized that landscape structure influences species composition at a particular site, most studies of management have focused on a single site, without taking into account the surrounding landscape (Saunders, Hobbs & Margules 1991; Kleijn & Verbeek 2000). However, insects have a better chance of finding suitable habitats, shelter or food over the course of a season in a mosaic of different grassland types. Furthermore, the destructive effect of mowing may be mitigated when different grassland types are present, as insects can escape to adjacent meadows where they may find new habitats. Indeed, both the sink–source model (Pulliam 1988; Howe & Davis 1991; Watkinson & Sutherland 1995) and the metapopulation concept (Harrison 1993; Reich & Grimm 1996; Hanski 1997) are theoretical concepts that recognize the essential role of dispersal for long-term persistence of organisms in patchy habitats. Moreover, as species differ in their responses to management, it is important to support a high diversity of management types in order to maintain and enhance species diversity at a regional level (Morris & Rispin 1993; Dietl 1995; Painter 1999).

This paper presents part of a study on the effects of both management and landscape structure on species diversity of agricultural grasslands in Switzerland. We chose the true bugs (Heteroptera) as an indicator group for insect diversity in general for various reasons. First, the bugs are an ecologically very diverse group, including phytophagous, saprophagous and predatory species (Dolling 1991). Furthermore, some species are generalists while other are specialists. Secondly, both larval stages and adults live in the same habitat and respond sensitively to environmental changes (Morris 1969, 1979; Achtziger 1995; Otto 1996). Thirdly, previous studies have shown that the richness of the bug fauna correlates strongly with total insect diversity (Duelli & Obrist 1998). Finally, and despite their ecological diversity, the Heteroptera is a manageable group in terms of the numbers of species occurring in grasslands.

In Switzerland different schemes have been developed to enhance biological diversity in agricultural systems. The aim of our study was to evaluate how contrasting grassland management techniques influence insect diversity in agricultural landscapes and to assess to what extent insect diversity of grasslands is affected by landscape structure. In this paper we focus on the effect of management on the species composition of the heteropteran fauna.

Materials and methods

RESEARCH AREA AND STUDY SITES

The research area was located in the Schaffhauser Randen (northern Switzerland; Table 1) and forms part of the hills of the Swiss Jura. The soils are nutrient-poor limestones. The average yearly precipitation in Schaffhausen (437 m a.s.l.) is 866 mm, the highest rainfall occurring in summer and the lowest in late winter. The average mean annual temperature is 7·8 °C, with maximum in July (23·2 °C) and minimum in January (–3·9 °C) (SMA 1998). The study site is an extensive forested region with several more or less isolated enclaves of agricultural land. Local agricultural policy encourages farmers to maintain extensive meadows by offering subsidies if they follow specified forms of grassland management.

For our study we chose a nested block design with two levels. At the block level (landscape type) we selected four enclaves (= areas) ranging in size from 30 to 240 ha with varying proportions of arable and grassland habitat. Within each block (area) we investigated two

Table 1. The four areas are situated in different communities of the Canton Schaffhausen. The altitude is given in metres above sea level. The area of the individual enclaves has been estimated based on 1 : 5000 maps

Area	Community	Altitude	Area of enclave	Coordinates
Zelgli/Mösli	Hemmental	800	30 ha	8°34′ E/47°45′ N
Hinterranden	Hemmental/Siblingen	830	40 ha	8°34′ E/47°44′ N
Klosterfeld	Hemmental	670	100 ha	8°36′ E/47°44′ N
Merishauser Randen	Merishausen	780–830	240 ha	8°36′ E/47°46′ N

grassland management types (intensive and extensive), and for each management type we selected three replicate sites. The management types were defined by two main factors: the number of cuts per year, and the type and amount of fertilizer used. Intensive meadows were regularly fertilized with slurry and were cut two to three times per year. The time of the first cut was approximately the end of May. The extensive meadows were not fertilized and were cut once or twice per year. The time of the first cut was July. We selected the grassland types on the basis of the plant species composition and later we interviewed the farmers about the amount and type of fertilizer used, the number of cuts, the time of cutting and the previous management. In these interviews we learnt that in the area of Hinterranden, the selected intensive grasslands had been managed in a less intensive way for the previous few years. The management contrast in this area was therefore smaller than in the other areas.

The plant species composition was assessed in summer 1997 using six randomly located $1 \times 1\text{-m}^2$ quadrats per site. A total of 110 plant species was recorded in the 24 sites, with the number of species sampled per site ranging from 21 to 48. The extensive and intensive meadows showed clear differences in plant species richness and in species composition. The community of the extensive meadows was dominated by *Bromus erectus* L. and there was a mean species number of 42 in the sample of six quadrats. The intensive sites were dominated by *Arrhenatherum elatius* L. and *Trisetum flavescens* L. and the mean species number was 30 (Studer 2000).

SAMPLING METHODS

The heteropteran bugs were sampled during the summer of 1997 using a standardized sweep-net method (Remane 1958; Bornholdt 1991; Otto 1996). The sweep-net had a diameter of 40 cm and was fitted with a heavy cloth suitable for sampling insects in the vegetation. Samples were collected every 2 weeks by making 100 sweeps with the net over a distance of about 100 m. The net was emptied after every twentieth sweep, resulting in five subsamples per site at each sampling date. Sampling was only carried out when the weather conditions were good, i.e. a minimum of 17 °C and sunshine. Sampling was also restricted to the period between 10:00 h and 17:30 h; the sampling order of the fields was varied between weeks. Each site was sampled between seven and nine times from May to September.

The adult insects were identified with the aid of entomological handbooks (Wagner 1952, 1966, 1967, 1970–71, 1975; Wagner & Weber 1964). The nomenclature followed Günther & Schuster (1990). All species identification was checked by R. Heckmann (Germany) and Ch. Rieger (Germany).

STATISTICAL ANALYSIS

For the analysis of the data, all samples were pooled over time, resulting in one sample per meadow. We used rank abundance distributions to compare the bug communities of the two management types because this method takes into account both species number and their abundance (Magurran 1988). Canonical correspondence analysis (CCA) (CANOCO, version 3·1; ter Braak 1987–92) was used to study the influence of management factors and spatial effects on the bug communities. The variance of the bug species data was partitioned into spatial (area) and management components (Borcard, Legendre & Drapeau 1992). The number of cuts, time of the first cut, and number of plant species sampled per meadow were included in the model as management variables. The four areas investigated (enclaves) were included as a spatial factor. The apparent species composition of communities is strongly influenced by sample size and rare species tend to be recorded only in large samples. To minimize sampling effects we omitted both rare species (< 3 individuals) and sites that were sampled fewer than eight times (three sites in the Merishausen area and one in the Hinterranden area). For the 24 most common species (> 14 individuals) analyses of variance were conducted to examine how individual species responded to management.

Results

INFLUENCES OF GRASSLAND MANAGEMENT ON INSECT DIVERSITY

A total of 5608 adult bugs comprising 93 species characteristic of meadows was recorded in the 24 sites (occasional vagrants from wooded habitats were excluded). In three of the four areas the bug communities of the extensive meadows demonstrated a more even rank abundance distribution than those of the intensive meadows (Fig. 1a–c), while in the fourth area (Hinterranden) the community structures were similar (Fig. 1d). The overall pattern in the intensive sites was for a few species to have a very high abundance, while the majority were less abundant than in extensive meadows. This contrast was clearest within areas, as the communities varied strongly from area to area.

The ordination model explained 72·3% of the total variance (total inertia 1·578; sum of all canonical eigenvalues 1·141; Monte Carlo permutation test $P = 0{\cdot}01$; Fig. 2). Of this, area accounted for 35·4% (eigenvalue 0·559, $P = 0{\cdot}01$) of the species variance, management accounted for 29·7% (eigenvalue 0·468, $P = 0{\cdot}01$) and the interaction management × area accounted for 7·2%. The plant species number was included with the variable 'management' and we therefore cannot say how much variation it explained.

The first and second axes (eigenvalues 0·554 and 0·191, respectively) of the ordination analysis (Table 2 and Fig. 3) accounted for 47·2% of the species variance, while the third and fourth axes (eigenvalues 0·158 and 0·077, respectively) for 14·9%. The ordination diagrams

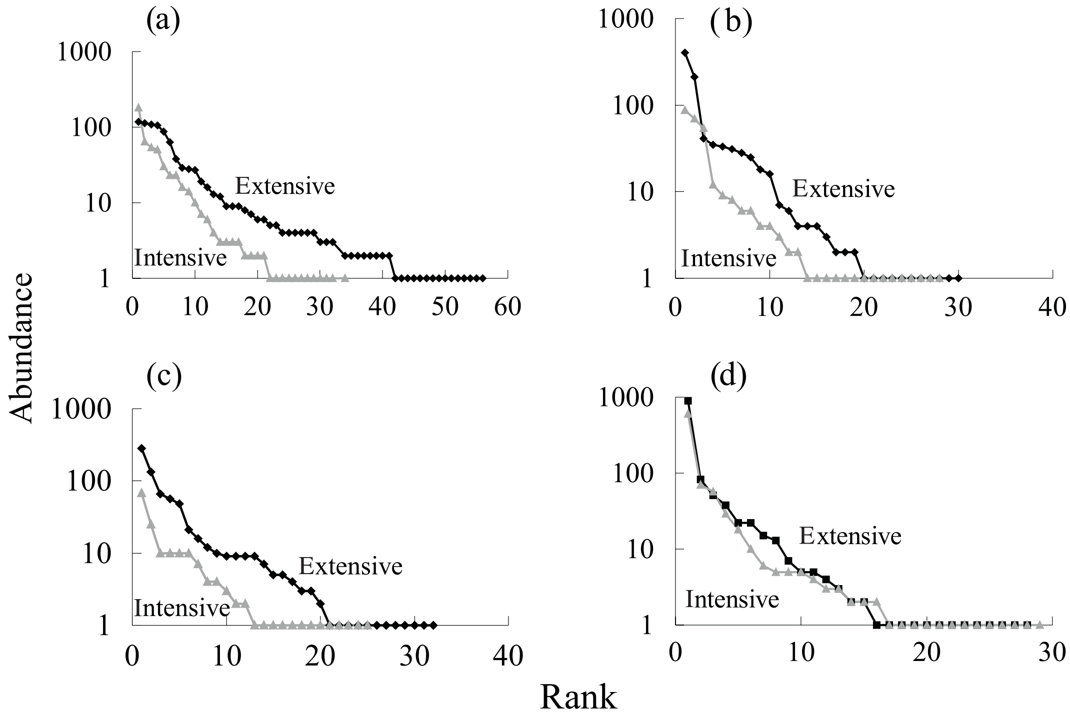

Fig. 1. Rank abundance distributions of heteropteran communities of extensively and intensively managed meadows in different areas: (a) Klosterfeld, (b) Zelgli/Mösli, (c) Merishauser Randen and (d) Hinterranden. Three sites per management type and area have been pooled for this analysis.

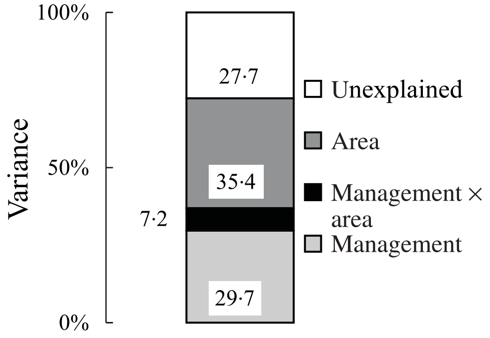

Fig. 2. Based on a canonical correspondence analysis, the species variance was partitioned into spatial (area) and management components. The ordination model explains 72·3% of the total variance (total inertia 1·578; sum of all canonical eigenvalues 1·141). Of this, area accounts for 35·4% (eigenvalue 0·559) of the species variance, management accounts for 29·7% (eigenvalue 0·468) and the interaction management × area accounts for 7·2% of the variance (see text for specifications).

show that axes one and two separated the Klosterfeld area from Hinterranden, and also the extensively managed meadows (July cut and one cut) from the more intensively managed ones (Fig. 3a). The extensive meadows are grouped in the upper part of the diagram of axes one and two, while the intensive ones are found in the lower part. The intensive sites are closely grouped, indicating that their heteropteran communities were very similar. Further, the extensive sites of Klosterfeld were separated from those of the other areas by the first axis. Hinterranden was clearly separated from the other areas by axes one and three, indicating that these sites had a markedly different species compositions (Fig. 3a,b). The plant species number was the only non-nominal variable in the model and was correlated with the first and second axes, although the correlation was not very strong (Table 2).

There was no significant correlation between the species number of plants and heteropteran bugs (t_{21} = 0·96, P = 0·35, R^2 = 0·04; Fig. 4).

SPECIES RESPONSE TO MANAGEMENT

At the species level, eight out of 24 species were significantly influenced by management. Because the timing of the first cut and the number of cuts were not independent variables we cannot be certain which factor was more important for the bug community. However, one or other factor usually correlated more strongly with the occurrence of species.

Only two species appeared to benefit more from intensive management, *Nabis pseudoferus* ($F_{2,20}$ = 3·55, P < 0·05) and *Notostira erratica* ($F_{2,20}$ = 4·57, P < 0·05), which were most abundant in intensive, frequently cut meadows (Fig. 5). There was evidence that *Nabis pseudoferus* was reduced by cutting in July ($F_{2,20}$ = 9·2, P < 0·01; Fig. 6).

Six species were affected adversely by intensive management. Of these, *Megaloceraea recticornis* ($F_{2,20}$ = 5·39, P < 0·05), *Peritrechus gracilicornis* ($F_{2,20}$ = 13·36, P < 0·001) and *Adomerus biguttatus* ($F_{2,20}$ = 3·96, P < 0·05) were apparently reduced by frequency of cut but not by the timing of the cutting. These species

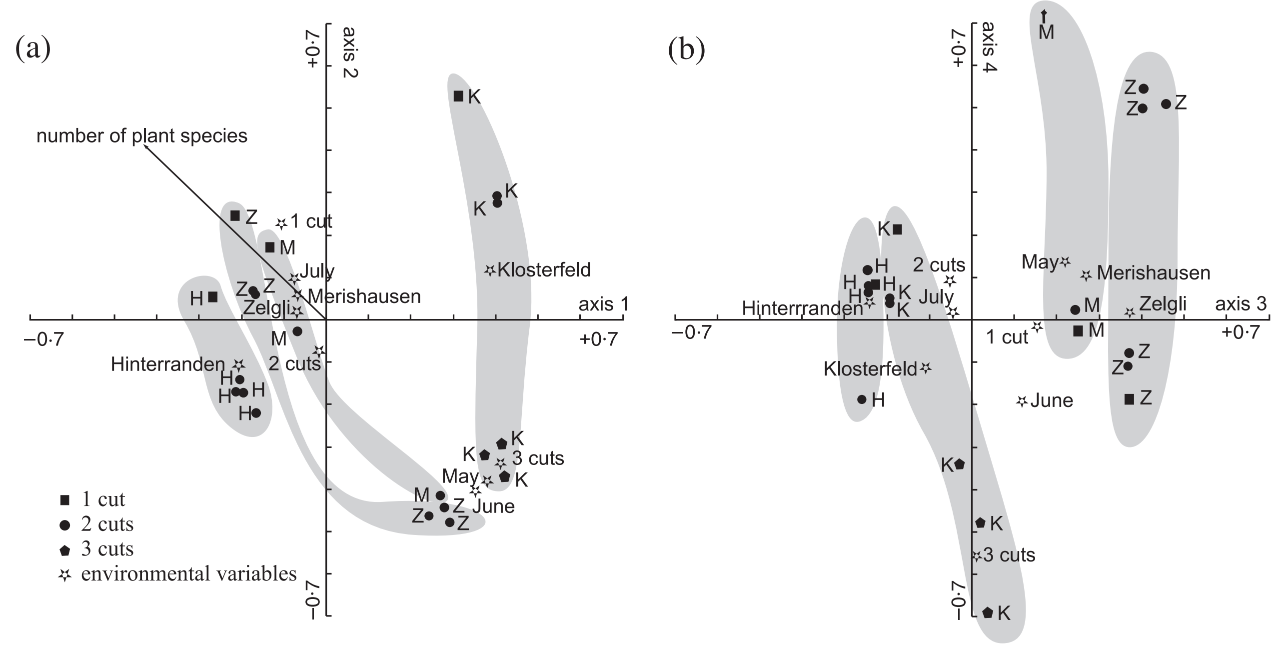

Fig. 3. Ordination diagrams based on a canonical correspondence analysis. Nominal variables are represented as points (centroids), non-nominal variables as vectors in the diagram. Different symbols are given for the number of cuts per year. The capital letters indicate the areas: Z, Zelgli/Mösli; K, Klosterfeld; M, Merishauser Randen; H, Hinterranden. Sites with similar species compositions and community structures are represented by points close to each other in the diagrams. Total inertia 1·578; eigenvalue first axis 0·554; eigenvalue second axis 0·191; eigenvalue third axis 0·158; eigenvalue fourth axis 0·077. The model was tested using a Monte Carlo permutation test: $P = 0{\cdot}01$. For this analysis four sites (three in Merishauser Randen and one in Hinterranden) were omitted because they were sampled less frequently than the other ones (see text for specifications).

Table 2. The correlation matrix is based on a canonical correspondence analysis and shows the values of the first four environmental axes

Variables	Environmental axis 1	Environmental axis 2	Environmental axis 3	Environmental axis 4
Area 1: Klosterfeld	0·8807	0·2660	−0·2635	−0·2660
Area 2: Zelgli/Mösli	−0·1488	0·0289	0·7723	0·0133
Area 3: Hinterranden	−0·6090	−0·3265	−0·7059	0·1146
Area 4: Merishauser Randen	−0·0983	0·0814	0·3996	0·1649
1 cut	−0·2656	0·6369	0·2167	−0·0080
2 cuts	−0·0469	−0·3609	−0·2097	0·3909
3 cuts	0·5121	−0·4222	0·0022	−0·6430
May cut	0·3777	−0·4323	0·2351	0·1534
June cut	0·4391	−0·4653	0·1505	−0·2255
July cut	−0·6070	0·666	−0·2832	0·0646
Number of plant species	−0·4240	0·4058	−0·001	0·0170

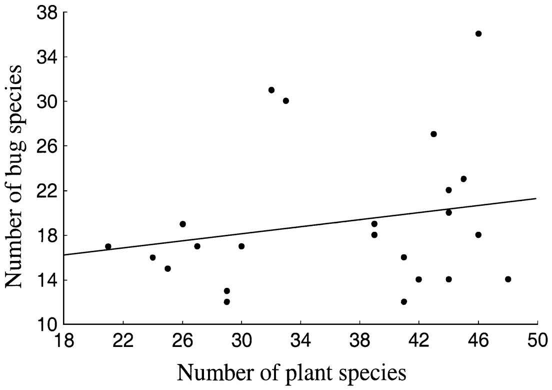

Fig. 4. The species number of plants and heteropteran bugs are not correlated ($t_{21} = 0{\cdot}96$, $P = 0{\cdot}35$, $R^2 = 0{\cdot}04$). Each point is for a different grassland site and is based on 6 1 × 1-m^2 quadrats for the vegetation and the recorded data for the bugs.

occurred most abundantly in extensive meadows (Fig. 5). The abundances of *Adelphocoris seticornis* ($F_{2,20} = 5{\cdot}0$, $P < 0{\cdot}05$; $F_{2,20} = 8{\cdot}19$, $P < 0{\cdot}01$), *Hadrodemus m-flavum* ($F_{2,20} = 13{\cdot}29$, $P < 0{\cdot}001$; $F_{2,20} = 4{\cdot}6$, $P < 0{\cdot}05$) and *Leptopterna dolobrata* ($F_{2,20} = 9{\cdot}26$, $P < 0{\cdot}01$; $F_{2,20} = 13{\cdot}95$, $P < 0{\cdot}001$) appeared to be reduced by both frequency of cutting and by early cuts (Figs 5 and 6).

Sixteen species showed no response to management intensity. These were *Lygus pratensis*, *Lygus rugulipennis*, *Dolycoris baccarum*, *Eurygaster maura*, *Carpocoris fuscispinus*, *Berytinus minor*, *Polymerus unifasciatus*, *Strongylocoris steganoides*, *Plagiognathus chrysanthemi*, *Stenodema laevigatum*, *Trigonotylus caelestialum*, *Adelphocoris lineolatus*, *Catoplatus fabricii*, *Nabis brevis*, *Chlamydatus pulicarius* and *Halticus apterus*.

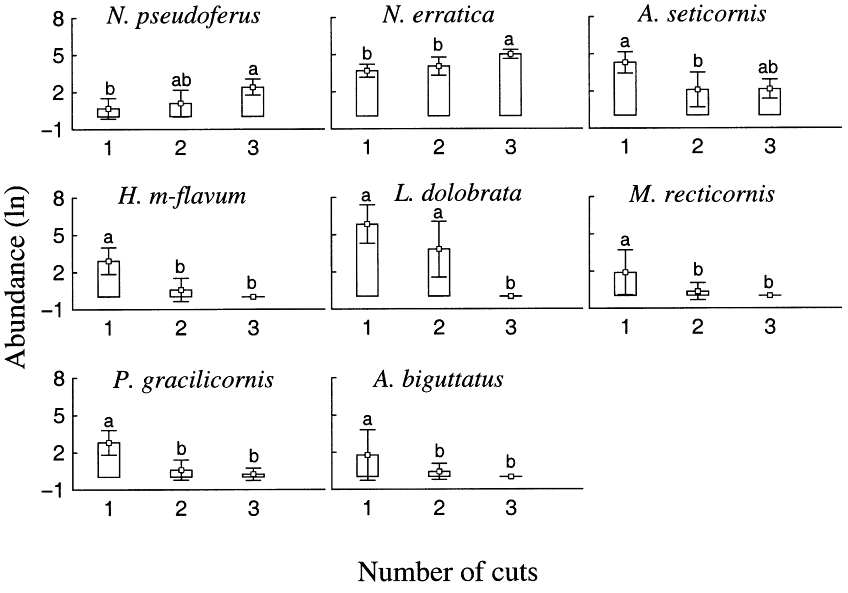

Fig. 5. Responses of individual species to the number of cuts (mean ± SD). The pairwise comparison was conducted with a Tukey test. Significant differences between the number of cuts are marked with different letters (a/b). *Nabis pseudoferus* ($F_{2,20}$ = 3·55, P < 0·05) and *Notostira erratica* ($F_{2,20}$ = 4·57, P < 0·05) are most abundant in frequently cut sites. In contrast, the abundances of *Adelphocoris seticornis* ($F_{2,20}$ = 5·0, P < 0·05), *Hadrodemus m-flavum* ($F_{2,20}$ = 13·29, P < 0·001), *Leptopterna dolobrata* ($F_{2,20}$ = 9·26, P < 0·01), *M. recticornis* ($F_{2,20}$ = 5·39, P < 0·05), *Peritrechus gracilicornis* ($F_{2,20}$ = 13·36, P < 0·001) and *Adomerus biguttatus* ($F_{2,20}$ = 3·96, P < 0·05) are reduced by frequent cutting.

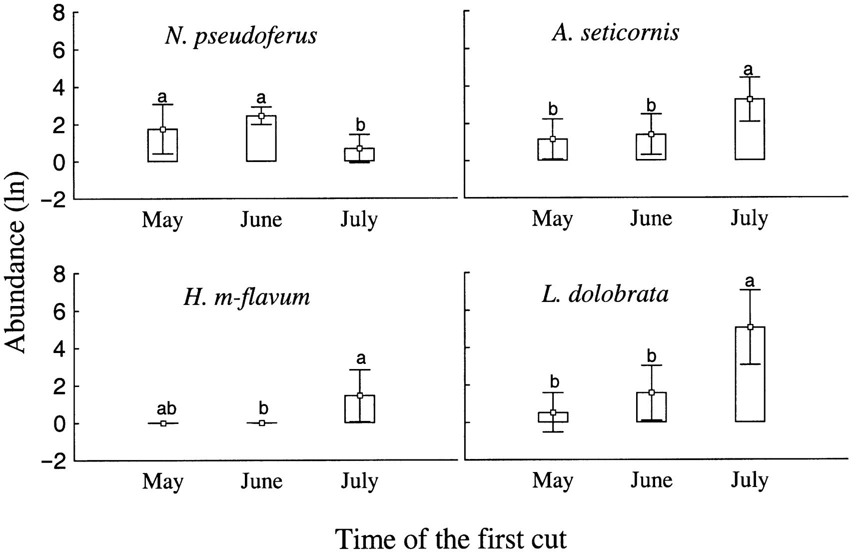

Fig. 6. Responses of individual species to the time of the first cut (mean ± SD). The pairwise comparison was conducted with a Tukey test. Significant differences between the time of cut are marked with different letters (a/b). July cut reduces the abundance of *Nabis pseudoferus* ($F_{2,20}$ = 9·20, P < 0·01). May and June cut reduces the abundances of *Adelphocoris seticornis* ($F_{2,20}$ = 8·11, P < 0·01), *Hadrodemus m-flavum* ($F_{2,20}$ = 4·6, P < 0·05) and *Leptopterna dolobrata* ($F_{2,20}$ = 13·95, P < 0·001).

Discussion

RESPONSES OF THE BUG COMMUNITY

The data presented here show that management effects are clearly important (Figs 2 and 3) for the species composition of the heteropteran bug community. They account for 30% of species variance and the ordination diagrams indicate that the extensive and intensive meadows have differing species compositions (Fig. 3a,b). The extensively managed meadows show a high variation in species composition, especially between areas, indicating that apart from management several other factors, such as aspect, light conditions and isolation, affect the species composition of these sites. The intensive sites, however, have very similar communities, suggesting that management is the most important factor influencing the species composition of these meadows. Further, species diversity tends to be greater in extensively managed meadows than in intensive ones. In three areas the extensive sites have more individuals and show a more even rank abundance distribution (Fig. 1a–c). One area (Hinterranden), however, is different. The rank abundance distributions (Fig. 1d) and the ordination diagrams (Fig. 3a,b) for Hinterranden show that the bug communities are very similar in both management types. As already mentioned, the intensive grasslands have been managed less intensively in the last few years. Interestingly, the vegetation does not reflect the recent changes in management so clearly and the species composition remains typical of intensive and extensive sites elsewhere (S. Studer, unpublished data); this suggests that the bug communities react more quickly than plants to management changes (Mortimer, Hollier & Brown 1998).

The environmental variables included in the CCA model explain most of the species variance (72·3%). The interaction term is very small (7·2%), indicating that the spatial and management variables are clearly separable in their effects (Borcard, Legendre & Drapeau 1992). Spatial effects account for an important part of the total variation (35·4%) and have a strong effect on the structure and assemblage of bug communities (Figs 2 and 3). It is not yet clear whether this is due to historical factors (e.g. differences in former land use) or to present day differences in landscape structure. However, the observation is consistent with various studies that show that geographical distributions of terrestrial invertebrates tend to be patchier, with more species having restricted ranges than is the case for terrestrial vertebrates and plants (Colwell & Coddington 1994; Otto 1996). The possibility that the structure of the landscape surrounding a site interacts with management effects on the insect community will be addressed in a more detailed spatial analysis of the data using Geographical Information Systems (GIS).

Interestingly, there is no correlation between the species number of plants and heteropteran bugs (Fig. 4) and only a weak relationship between plant species number and the species composition of the bug fauna as represented in the CCA (Table 2 and Fig. 3a,b). Our findings are supported by the study of Otto (1996), who showed that the heteropteran fauna is significantly correlated with the structure of the plant community but not with species richness. Apparently the bug fauna is affected more strongly by the structure and the microclimatic conditions in the grasslands than by plant species richness *per se*. As many bug species are zoophagous or polyphagous herbivores the plant species richness might play a less important role than the structural diversity of the habitat.

RESPONSES OF INDIVIDUAL SPECIES

Although the trends associated with management are clear, species do differ in their responses to management, and not all are adversely affected. For example, *Notostira erratica* is most abundant in intensive meadows (Fig. 5). This mirid bug has at least two generations per year. It feeds on grass leaves and can find its food even in freshly cut meadows. It is not yet clear how this species survives the frequent disturbances by cutting. It may be that it recolonizes meadows soon after the cut (Remane 1958; Morris 1969, 1979; Gibson 1980; Otto 1996). Bockwinkel (1990) has shown that at least a proportion of the adults takes shelter in adjacent meadows. If this is the case, then it is rather surprising because the females are very weak fliers due to their reduced flight muscles. The males, in contrast, are good fliers and seem to be quite mobile (Kullenberg 1944; Dolling 1991).

Nabis pseudoferus is a macropterous nabid with two to three generations per year that lives in various habitats, e.g. grasslands, cereals fields and field margins (Remane 1958; Southwood & Leston 1959; Péricart 1987). It is a predatory species that feeds mostly on smaller insects (Péricart 1987). Little is known about its biology, although it appears to benefit from intensive management and is more abundant in the intensive grassland sites (Figs 5 and 6). Macropterous nabids are often associated with ephemeral habitats and seem to be fast and strong fliers (Southwood 1960). In general, insect species with several generations per year have a better chance of persisting in highly disturbed habitats than those with only one (Southwood 1960; Morris 1979). This appears to be the case for both *Notostira erratica* and *Nabis pseudoferus*. In contrast to these species, *Megaloceraea recticornis* is severely reduced by cutting and is more abundant in extensive meadows (Fig. 5) or fallow land with a high proportion of grasses (Morris 1979; Otto 1996). Larval development takes place in spring, when the intensively managed grasslands are cut for the first time. This phase is the most sensitive of the whole life cycle and so susceptible to disturbances. The life cycle may therefore explain the sensitivity of the species to intensive management. Moreover, this species is a poor flier and therefore may be slow to colonize new habitats (Southwood 1960).

It is known that *Leptopterna dolobrata* does not occur on very poor soils (Kullenberg 1944) and that nitrogen is a factor that limits its larval development (McNeill 1973; McNeill & Southwood 1978). We might expect that intensively managed meadows with a high nitrogen availability would be a favourable habitat for this species. However, frequent and early cutting reduces this species severely (Figs 5 and 6) and the life cycle may be the critical factor. Because the females lay their eggs on the bottom part of grass stems (Kullenberg 1944), damage to the eggs is probably not the reason that it is restricted to extensive sites. Larval development, however, may be the critical phase because this takes place in June when the intensive meadows are cut (Kullenberg 1944; Wagner 1952; Southwood & Leston 1959).

Peritrechus gracilicornis is restricted to extensively managed meadows (Fig. 5). It is a lygaeid bug that occurs in warm, dry places (Wagner 1966), although little more is known about its biology. The heterogeneous and open vegetation of extensive sites provides a warm and dry microclimate on the ground and therefore ideal conditions for xerothermophilic species (Otto 1996).

Adomerus biguttatus is also a xerothermophilic species and therefore favoured by extensive management (Fig. 5). Moreover, it lives on *Melampyrum* where it feeds mostly on the roots (Southwood & Leston 1959; Wagner 1966). It is therefore restricted to the habitats of its host-plant, which is found in extensive but not in intensive meadows (Lauber & Wagner 1996).

Hadrodemus m-flavum is a monophagous species that lives on *Salvia pratensis* (Wagner 1952; Southwood & Leston 1959). Like its host-plant, it is restricted to extensively managed meadows (Figs 5 and 6). This species, too, overwinters as an egg and develops in early summer (Southwood & Leston 1959), therefore early cutting may damage the larval stages. *Adelphocoris seticornis* lives on *Vicia* species and is reduced by frequent and early cutting (Figs 5 and 6). The females lay their eggs in the upper part of the host-plant stem and larval development begins in spring (Kullenberg 1944; Wagner 1952; Southwood & Leston 1959). Cutting in May or June therefore may destroy its eggs or damage the larval stages.

For the species that do not appear to respond to management, two main groups can be identified. (i) Widespread species, which occur in various types of habitats: *Lygus pratensis*, *Lygus rugulipennis* (Southwood & Leston 1959; Morris 1979), *Carpocoris fuscispinus* (Wagner 1966), *Dolycoris baccarum* (Wagner 1966), *Trigonotylus caelestialum* (Remane 1958; Otto 1996), *Adelphocoris lineolatus* (Kullenberg 1944; Southwood & Leston 1959), *Stenodema laevigatum* (Wagner 1952; Remane 1958; Otto 1996), *Polymerus unifasciatus* (Kullenberg 1944; Wagner 1952), *Eurygaster maura* (Southwood 1960) and *Nabis brevis* (Southwood 1960; Péricart 1987). (ii) Polyphagous species, which live in a wide range of grasslands and which show a certain affinity to managed meadows: *Chlamydatus pulicarius* (Otto 1996), *Halticus apterus* (Kullenberg 1944; Otto 1996), *Plagiognathus chrysanthemi* (Kullenberg 1944; Morris 1979; Otto 1996), *Catoplatus fabricii* (Péricart 1983; Otto 1996) and *Berytinus minor* (Péricart 1984; Otto 1996).

In conclusion, this study shows that extensively managed meadows can be species-rich habitats and valuable for specialized insect species. In contrast, the bug community of intensive meadows is dominated by more widespread and less specialist species. Frequent and early cutting reduces the abundance of many species, and especially certain specialized or rare species like the xerothermophilic element of the Swiss bug fauna. The more widespread species, however, do not show a consistent response to management and some may even benefit from intensive management. Our results indicate that the extensive management of grasslands, as supported by agricultural schemes in Switzerland, is effective in maintaining insect diversity in agricultural landscapes. In our study we have mainly investigated management techniques that are used in practice, and we therefore cannot say whether there are other management techniques that would support even more species. Moreover, our study reveals that the extensively managed meadows can vary greatly in respect to their species composition, suggesting that to maintain species richness on a landscape level it is crucial to preserve a range of sites in various regional locations.

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