

Do they ever come back? Responses of leafhopper communities to extensification of land use

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Abstract

We studied leafhopper communities in meadows subject to progressive extensification of land use, particularly (i) delay of the first cut, (ii) cessation of fertilising and (iii) reduction of cutting events. Within a gradient from conventionally used high-productivity meadows (as control) through our extensified plots to extensively managed wet hay meadows (as control), we found an increasing species number correlated with extensification of land use. However, a separate analysis of generalists and specialists showed that the latter group increased significantly whereas generalists did not respond at all. Even after 12 years of extensification there was only little evidence for the recovery or recolonisation of former hay meadow insect communities. Instead the increase in species numbers was rather due to immigration of more xerophilous or mesophilous species. We conclude that leafhoppers principally respond positively to extensification of land use, but that restoration of former moisture conditions is necessary in order to achieve a full recovery of original hay meadow communities. Finally we propose a model extensification ecogram for meadow leafhoppers which can be used as a predictive tool for extensification and as an indicator of restoration progress and success.

Introduction

Anthropogenic grassland ecosystems in Europe often support a high biodiversity, which has developed since man began to raise cattle and to cut grass with sickles since the Neolithic (Curry 1987, 1994; Körber-Grohne 1990; Pott 1995; Ellenberg 1996; Siemann et al. 1999). Not later than the middle of the last century, many countries have noticed a decline of species diversity in these habitats, which was correlated with changes in land use (see Watkinson and Ormerod 2001; Biedermann et al. 2005). Firstly, widespread

intensification took place, often supported by large-scale drainage, resulting in an increase of organic and mineral fertilisation, mowing frequency, grazing intensity, and even application of pesticides. Secondly, areas less suitable for intensification were abandoned, thus becoming subject to secondary succession eventually leading to reforestation. Furthermore, large areas were ploughed, leading to an ultimate loss of habitats and enforcing fragmentation of the remaining patches (Tschardtke and Brandl 2004).

During the 1970s and 1980s, some European governments developed conservation programs to

stop the decline of grassland species and to restore meadow communities by extensification of land use (e.g. reduction of mowing intensity and fertilisation). The main approach was to sign contracts with farmers who, for monetary compensation, refrained from high-intensity land use. The aim of these measures was to preserve and recover grassland communities, many of which include high proportions of specialised or threatened plants and animals. In most cases target species were grassland birds such as great bustard (*Otis tarda*), curlew (*Numenius arquata*), redshank (*Tringa totanus*) and other waders (Olsen and Schmidt 2004), and some invertebrate groups such as butterflies, ground beetles or grasshoppers (Dolek and Geyer 1997; Wettstein and Schmid 1999; Kruess and Tschardt 2002; Brose 2003). Leafhoppers (this term used here as a synonym for all Auchenorrhyncha, i.e. including planthoppers), have only relatively recently been treated not only as indicators for habitat conditions and disturbance intensity (Andrzejewska 1965; Morris 1981a, b; Achtziger and Nickel 1997; Achtziger et al. 1999; Niedringhaus 1999; Morris 2000; Bornholdt 2002; Nickel and Hildebrandt 2003; see Biedermann et al. 2005), but also as conservation objects themselves (Kirby 1992; Remane et al. 1998; Nickel 2004). In contrast to other insects which are more mobile, their close association with their host plants allows a high spatial resolution (e.g. Novotný 1994; Achtziger 1999; Nickel 2003).

In order to evaluate the efficiency and success of such an extensification program, the Bavarian Agency for Environmental Protection initiated investigations of several animal groups, which included not only birds, but also other target and potential prey groups such as butterflies, grasshoppers, true bugs and leafhoppers (Achtziger et al. 1999; Kriegbaum 1999). In this paper we re-analysed our data to see how they could be related to insect conservation, addressing the following questions: (i) How does conventional management affect insect communities in meadows? (ii) Is the extensification of land use intensity an efficient tool for the recovery of typical and species-rich insect communities, and how much time is necessary? (iii) Which species of leafhoppers can be expected to recolonise extensified meadows? The practical application of our results will be discussed in order to offer guidelines for meadow grassland management, which have hitherto been

largely derived from floristic or avifaunistic evidence.

Study area

The field work was conducted in 1995 and 1996 in the floodplains of two tributaries of the upper Danube in Bavaria (southeastern Germany), where cattle are usually housed indoors, and thus, grassland is predominantly used as meadows. The first area is the Wiesmet floodplain (hereafter abbreviated as WF) situated in the upper reaches of the Altmühl river near the village of Ornbau at 415 m. The second area is the Königsauer Moos (abbreviated as KM), situated in the Isar floodplains to the northeast of the city of Dingolfing at 350 m. In general, land use intensity is higher in KM which is a former floodplain mire much degraded through anthropogenic drainage and subsequent mineralisation of peat. Further, study plots in KM showed, compared to WF, significantly higher mean nutrient supply (average Ellenberg's nitrogen values of vegetation), total carbon contents (reflecting degradation of turf), pH-values, and had a significantly lower moisture (average Ellenberg's moisture value of vegetation) (see Achtziger et al. 1999). As a consequence WF is spatially rather diverse and rich in grassland birds, whereas KM is rather monotonous, with fewer grassland bird species.

Study plots were grouped according to the type of compensation contract with farmers (Table 1). The principal idea of the contract model was to allow only late mowing (not before June 20th) in order to prevent destruction of nests and killing of young birds (contract type 'Extensification level 1', abbreviated as 'E1'). In addition, fertilising was prohibited in some plots (contract type 'Extensification, level 2', abbreviated as 'E2'). Whereas both these contract types allowed as many cuts as possible a year (usually no more than 2), a third type ('Extensification, level 3', abbreviated as 'E3') allowed no more than a single cut at different dates, with a narrow strip mown only every two years. Furthermore, some plots were kept as fallows without annual mowing and fertilising. As control plots we chose non-contract meadows subject to conventional (i.e. intensive) treatment as well as protected hay meadow remnants, which had never been subject to intensive use nor to

Table 1. Land use and contract regulations for study plots (KM = Königsauer Moos, WF = Wiesmet floodplain).

| Land use/contract type | Abbreviation | Mowing regime | Fertilising | Contract duration | n plots/study year |
|----------------------------------|--------------|--|----------------|-------------------|-------------------------------------|
| Conventional/Intensive (control) | Int | Not restricted, usually early June, usually at least 3 cuts a year | Not restricted | – | 2/1995 (KM) 2/1995 (WF) 2/1996 (WF) |
| Extensification I | E1 | Not before June 20 (KM) or July 1 (WF), at least 2 cuts | Not restricted | 1–12 years | 6/1995 (KM) 5/1995 (WF) |
| Extensification II | E2 | Not before June 20 (KM) or July 1 (WF), usually 2 cuts | Not allowed | 5–11 years | 6/1995 (KM) 7/1995 (WF) |
| Extensification III | E3 | Differentiated, no more than 1 cut (see text) | Not allowed | 6 years | 10/1996 (WF) |
| Fallow | F | Not every year | Not allowed | – | 3/1996 (WF) |
| Hay meadow (control) | Ext | Partially in autumn | Not allowed | – | 2/1995 (KM)/ 1995 (WF) 2/1996 (WF) |

anthropogenic drainage, and which are mown only every few years in autumn for conservation purposes. An overview of the sample plots and their treatments is given in Table 1.

For the extensified contract plots (E1, E2) sampled in 1995, data of plant species composition, total vegetation cover, coverage of plant families, vegetation height, and some soil parameters (pH, C/N ratio, total carbon content) were available (see Fischer 1999). Plant species data allowed us to calculate mean Ellenberg's indicator values of moisture and nitrogen for each plot (see Ellenberg 1996).

Methods

Insects were sampled on two dates (second half of June and end of August to beginning of September 1995 and 1996) with standardised sweep-net catches. The sweep-net frame was nearly square, measuring 30×30 cm. We made 100 sweeps, walking diagonally through the plot. In addition, after each sweep-net sampling we directly searched for epigeic species for about 5–10 min, depending on the structural complexity of the plot. These additional catches were only included in the analysis of numbers of species, but not of individuals. Catches were transferred to plastic bags and frozen.

For the analysis of responses to land use intensity, we categorized species according to their life strategy type based on the r- and K-concept (Pianka 1970; Grime 1973), using host plant range, habitat requirements, annual generation number and mobility (deduced from wing length), see Table 2.

We used Statgraphics Plus 5.0 (Statistical Graphics Corp. 1994–2000) and Sigmastat 2.0 (Jandel Corporation 1992–1995) for statistical data analysis. In cases of low sample size and/or lack of normal distributions, we chose non-parametric tests. For the ordination of communities the Nonmetric Multidimensional scaling (NMDS) procedure of NTSYS 1.5 (Rohlf 1988) was used. As distance measure Wainstein indices were calculated, which is the product of Renkonen index and Jaccard value (Wainstein 1967), allowing a consideration of both similarity of dominance structure (by Renkonen index) and species identity (by Jaccard index) (Mühlenberg 1993). As initial

Table 2. Life strategies of grassland leafhoppers, modified after Achatziger and Nickel (1997) and Nickel and Hildebrandt (2003), species data from Nickel (2003).

| Life strategy classification | Range of habitat preference | Wing length/flight activity | Diet width | Annual generation number* |
|------------------------------|--|---|-------------------------------------|---------------------------|
| Generalists | | | | |
| Pioneer species | Wide, but most abundant in early succession habitats | Always long-winged; permanent influx into most terrestrial habitats | Polyphagous or broadly oligophagous | 2 or more |
| Eurytopic species | Wide, but largely absent from early succession sites | Long- or short-winged, flight activity moderate | Usually oligophagous | Usually 2 |
| Specialists | | | | |
| Oligotopic species | Moderate to narrow | Long- or short-winged, flight activity moderate | Usually oligophagous | 1 or 2 |
| Stenotopic species | Narrow | Mostly short-winged; flight activity usually low | Monophagous | 1 or 2 |

*May be subject to geographic variation.

configuration matrix for NMDS we used the results of a Principle Coordinates Analysis (PCoA) within NTSYS.

In order to detect significant differences in community composition between land use intensity categories, we performed multi-response permutation procedures (MRPP) (Zimmerman et al. 1985) within the program package PC-ORD 4.10 (McCune and Mefford 1999). MRPP is a non-parametric procedure which tests the hypothesis of no difference between two or more *a priori* groups of entities (McCune and Mefford 1999), e.g. land use categories. For MRPP we used Bray-Curtis distance measure and a group weighting recommended by Mielke (1984).

PC-ORD was also used to calculate indicator values for species (Dufrêne and Legendre 1997), based upon both a species' relative abundance in a given habitat as well as its fidelity to that habitat in correspondence to pre-defined groups of sites (here: land use categories). This indicator value ranges from 0 to 100% (=perfect indication). The significance of the maximum indicator value was estimated by Monte Carlo test (1000 permutations) within the PC-ORD procedure.

Our Auchenorrhyncha moisture index (AMI), which is used here as a surrogate parameter for soil moisture, is based on field data from all over Germany (Nickel and Achatziger 1999; Nickel 2003). It corresponds to Ellenberg's indicator value for moisture requirements of plants (see Ellenberg 1996), which ranges from 1 (=extremely dry) to 12 (=permanently flooded), except that

AMI maximum in managed grassland is only at 9.5. In 11 of our WF plots for which plant data were available AMI was significantly correlated with Ellenberg's moisture value ($r = 0.82$, $p = 0.002$).

Results

Species numbers

In total we found 15,900 individuals belonging to 91 species of leafhoppers (see Appendix Table), which represent about 75% of the 120 species known to live in managed grasslands of central Europe (Nickel and Achatziger 1999; Nickel 2003). In the Wiesmet floodplain 72 species were recorded, which included 9 species of the Bavarian Red List of threatened animal species. In the Königsauer Moos 59 species were found including 6 of the Red List. In both regions a large proportion of the species total was found only in extensively managed hay meadows (Wiesmet floodplain 33 spp., Königsauer Moos 33 spp.).

Species numbers per study plot ranged from 5 in an extensification level I (E1) plot to 28 in a control hay meadow. In both regions and study years, mean species numbers were lowest in intensive control plots (Int), they increased in E1, through E2 and E3 plots, and were highest in control hay meadows (Ext) (Table 3). Based on Dunn's test following a Kruskal-Wallis test, differences were significant between wet hay meadows on the one

Table 3. Average species numbers of leafhoppers in response to land use intensity. Mean \pm standard deviation; different letters indicate significant differences between intensity categories (Kruskal–Wallis test, Dunn’s test).

| Study region/year | Intensive | Extensive level 1 | Extensive level 2 | Extensive level 3 | Fallow | Extensive wet hay meadow |
|-------------------------|------------------------------|-------------------------------|-------------------|-------------------|-------------------------------|-------------------------------|
| Wiesmet floodplain 1995 | 8.00 ^a \pm 1.41 | 10.00 ^b \pm 2.90 | 12.57 \pm 1.62 | – | – | 15.67 ^c \pm 2.08 |
| Wiesmet floodplain 1996 | 9.00 ^a \pm 1.41 | – | 14.25 \pm 2.22 | 15.30 \pm 2.16 | 13.33 ^a \pm 3.06 | 24.50 ^b \pm 4.95 |
| Königsauer Moos 1995 | 13.00 \pm 0.00 | 13.67 \pm 2.66 | 16.00 \pm 2.97 | – | – | 25.00 \pm 2.83 |

hand and Int (WF 1995/96) and E1 (WF 1995) plots on the other hand (WF 1995). Species numbers in fallows (WF 96) were higher than in Int and E1 plots, but not significantly. In KM, significant differences were found only at the 10% level (Kruskal–Wallis test, $p = 0.07$).

In summary, species numbers increased with decreasing land use intensity. In both regions, we could not find any significant correlation of leafhopper species numbers with plant species number per plot nor with any other recorded parameter of vegetation or soil.

Community structure

If we classify leafhopper species according to their life strategies (Table 2), the resulting pattern is somewhat different: Generalists (pioneer species and eurytopic species) are more or less equally diverse in intensively managed control plots (Int) and in all three contract variants (E1, E2, E3), and there is even a slight decrease in fallows (F) and hay meadows (Ext) (Figure 1, white columns). In contrast, diversity of specialists (oligotopic and stenotopic species) increased gradually with decreasing management intensity, i.e. from Int plots through intensified (E1, E2, E3), F and Ext plots (Figure 1, black columns). Differences of mean species numbers of specialists were significant between Int or E1 plots on the one hand and Ext plots on the other hand (Kruskal–Wallis test, Dunn’s test).

We conclude that the reduction of fertilising and mowing causes an increase in species numbers. This response is almost exclusively accounted for by specialists, whereas the response by generalist species is indifferent or even opposite. A similar, but even clearer pattern arises when regarding Red List species, most of which are specialists. In both areas all but a single species were exclusively confined to hay meadow control plots (see Appendix Table).

This shift from species-poor leafhopper communities dominated by pioneers and eurytopic species in conventional meadows to diverse communities with high numbers of oligotopic and stenotopic species is illustrated in Figure 2. According to Hengeveld (1996) who postulated a more detailed analysis of animal communities for measuring ecological diversity, such ‘diversity spectra’ indicate not only changes in mere species numbers but also in ecological diversity.

In order to analyse the distribution of single species and to identify indicator species for different intensification levels we calculated indicator values after Dufrêne and Legendre (1997) from data collected in 1996 in the Wiesmet floodplain. Out of 18 species analysed we found highly significant values for a single land use category in 5 species, and significant values in 4 species (Table 4).

As expected, pioneer species, e.g. *Macrostes sexnotatus*, *M. laevis*, *Psammotettix alienus* and – to a lesser extent – *Javesella pellucida*, were found essentially in intensively managed meadows, which can be quickly recolonised after each disturbance event (Table 4). At the other end of the intensity gradient, specialists such as *Sorhoanus assimilis* (on *Carex* spp.), *Macrostes septemnotatus* (on *Filipendula ulmaria*) and many other species with low densities (see Appendix Table) were restricted to hay meadows (Table 4). Eurytopic species were found mainly in intensified sites and/or fallows: For example, *Deltocephalus pulicaris* and *Arthaleus pascuellus* on E2 plots, *Errastumus ocellaris* and *Philaenus spumarius* on E3 plots and/or fallows (Table 4). *Cicadella viridis* and *Forcipata citrinella* were sampled either on intensified plots (E2, E3) or in hay meadows, but not in fallows (Table 4). Though regarded as specialists, *Cicadula quadrimotata* and *Euconomelus lepidus* could be found on some intensified E2 or E3 plots where their host plants occurred (*Carex* spp., *Eleocharis* spp.).

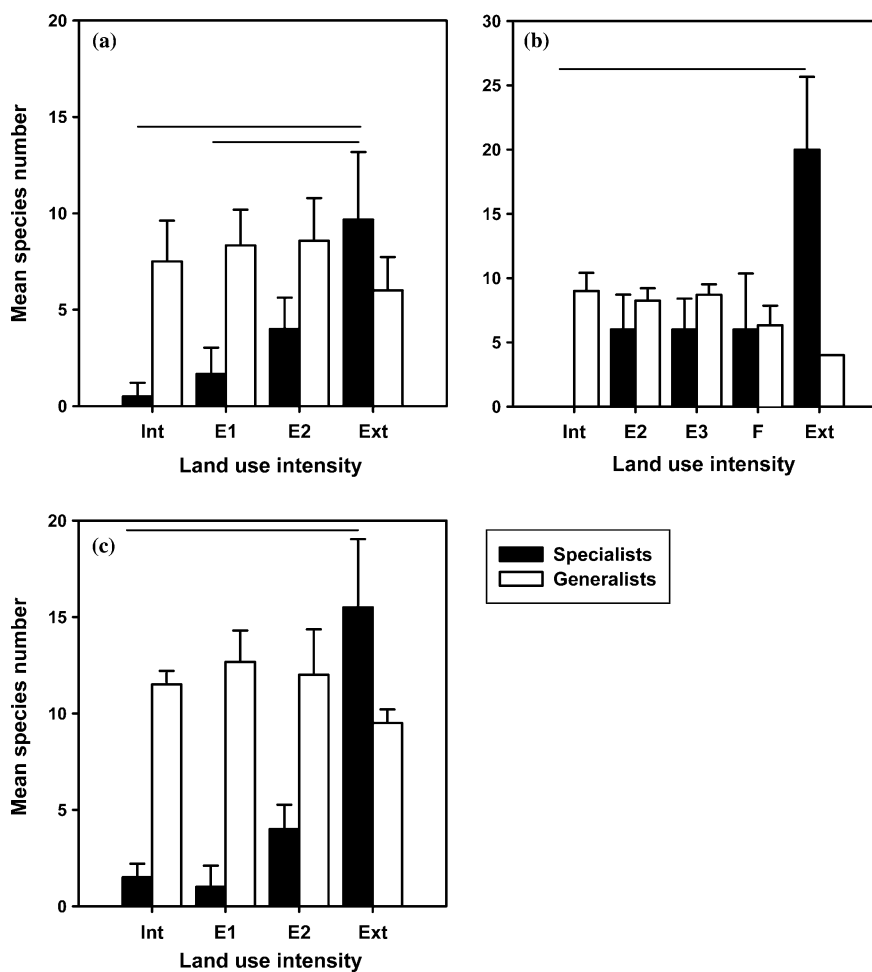


Figure 1. Mean numbers of specialist (black columns) and generalist species (white columns) of leafhoppers per land use type in (a) Wiesmet floodplain 1995, (b) Wiesmet floodplain 1996, and (c) Königsauer Moos 1995. Error bars are standard deviations, horizontal lines indicate significant differences between groups (Dunn's test).

The effects of land use extensification on community structure can be seen in an NMDS ordination of leafhopper communities of different plots in the Wiesmet region (Figure 3): It shows a general change visualised by a more or less straight tendency from left to right along axis 1, with only some overlap of succeeding extensification variants. The extensively managed wet hay meadows situated in the lower right corner do not show any overlap with other variants and were separated along axis 2. The Auchenorrhyncha moisture index (AMI), indicated by the size of the data points, is correlated with NMDS axis 1 ($r = 0.64$, $p < 0.001$, $n = 39$), but even better with axis 2 ($r = 0.70$, $p < 0.0001$, $n = 39$), indicating a higher moisture level in our hay meadow plots. The

increasing proportion of hygrophilic species can be interpreted as the potential effect of rewetting. The described shift in species composition along the restoration gradient is also consistent with the results of multi-response permutation procedures (MRPP) which show significant differences in community composition between land use categories (test statistics $T = -7.858$, $p < 0.001$).

Effects of length of the extensification period

There was a significant positive effect of contract (i.e. extensification) duration on individual and species numbers of leafhopper specialists in E2 plots of the Wiesmet floodplain (individual

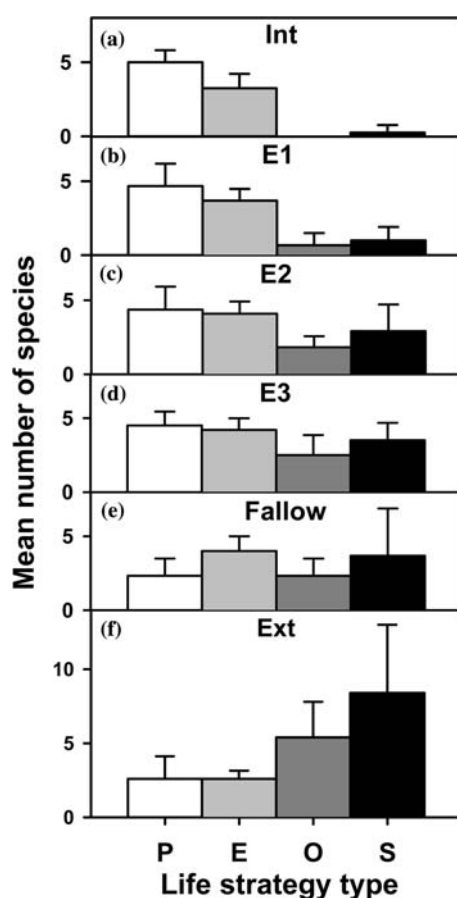


Figure 2. Leafhopper species numbers and their life history traits (diversity spectra) on meadows subject to different land use intensity in the Wiesmet area (error bars = standard deviations, P = pioneer species, E = eurytopic species, O = oligotopic species, S = specialists, for definitions see Table 2, for numbers of plots see Table 1).

numbers: see Figure 4; species numbers: $r_s = 0.74$, $p = 0.07$, $n = 7$). Probably due to small sample sizes, no such correlation could be found for E1 plots nor for any of the variants studied in the Königsauer Moos.

Discussion

Effects of meadow treatment on insect communities

Modern conventional management of meadows includes mowing, mineral fertilising, and, locally, rotational grazing and application of pesticides. The low species number on our conventional control plots (Figure 1) suggests that this man-

agement has an adverse effect on leafhopper species richness in grasslands. Simplification and impoverishment of leafhopper communities in intensified grassland have also been reported from numerous studies in other parts of Germany (Marchand 1953; Remane 1958; Nikusch 1976; Nickel and Hildebrandt 2003), Poland (Andrzejewska 1991) and the UK (Helden and Leather 2004) and have been shown to be a general phenomenon also reported from numerous other grassland invertebrates (e.g. Morris and Plant 1983; Curry 1994; Wettstein and Schmid 1999; Di Giulio et al. 2001), birds (Benton et al. 2003; Olsen and Schmidt 2004) and plants (e.g. Ellenberg 1996; Smith et al. 2000; Rajaniemi 2002).

Detailed studies were also conducted in order to identify the role of single factors. In a 2-year study in the UK, Prestidge (1982) found positive effects of NPK fertiliser treatment on the total number of individuals. There were no effects on species numbers, but 5 (out of 26) species declined significantly in numbers. In a 3-year study conducted in Poland, Andrzejewska (1976) found almost equal densities in fertilised and untreated control plots, but species numbers declined in NPK fertilised plots. In a long-term experiment at Rothamsted, UK, in plots with constant treatment for more than 100 years, Morris (1991) did not find significant differences in total individual numbers between N-fertilised and control plots, but species numbers were significantly higher in the latter.

The precise mechanism is not yet clear, but may be dessication of insects through direct contact with fertilisers or, as suggested by Curry (1994), impoverishment of the vegetation and loss of certain host plants. Even if there are no direct effects on a particular leafhopper species, it may become affected through an increase in mowing incidents caused by fertilising. In any case, there is convincing evidence that mineral fertilising leads to a general decline in species diversity of grassland leafhoppers. It is conceivable that exceptions occur during initial improvement of sites on extremely poor soil, such as peat or sand, where fertilising could increase plant biomass and species number, and thus, resources available to phytophages. Such a case has been reported more recently from a hemipteran community in a Scottish upland moor (Hartley and Jones 2003).

Mowing has been identified as another important factor which negatively affects leafhopper

Table 4. Indicator values of leafhoppers for land use types in the Wiesmet floodplain 1996 (only species recorded in more than 30 individuals). Significant indicator values are shown in bold; p = significance of maximum indicator value (Monte-Carlo-Test, 1000 permutations).

| Species | Indicator value | | | | | p |
|--------------------------------|-------------------|---------------------|---------------------|--------|------------|-------|
| | Intensive control | Extensified level 2 | Extensified level 3 | Fallow | Hay meadow | |
| Pioneer species | | | | | | |
| <i>Macrostes sexnotatus</i> | 83 | 10 | 6 | 0 | 0 | 0.004 |
| <i>Macrostes laevis</i> | 68 | 9 | 16 | 0 | 0 | 0.001 |
| <i>Psammotettix alienus</i> | 70 | 3 | 14 | 2 | 1 | 0.002 |
| <i>Javesella pellucida</i> | 31 | 34 | 29 | 1 | 0 | 0.170 |
| <i>Psammotettix confinis</i> | 5 | 26 | 47 | 7 | 1 | 0.004 |
| Eurytopic species | | | | | | |
| <i>Deltocephalus pulicaris</i> | 10 | 59 | 16 | 1 | 0 | 0.035 |
| <i>Arthaldeus pascuellus</i> | 2 | 55 | 26 | 14 | 3 | 0.001 |
| <i>Philaenus spumarius</i> | 2 | 17 | 31 | 24 | 27 | 0.657 |
| <i>Errastunus ocellaris</i> | 5 | 5 | 49 | 32 | 0 | 0.173 |
| Oligotopic species | | | | | | |
| <i>Aphrodes bicincta*</i> | 0 | 1 | 47 | 27 | 5 | 0.333 |
| <i>Cicadella viridis</i> | 0 | 31 | 6 | 0 | 39 | 0.315 |
| <i>Neophilaenus lineatus</i> | 0 | 0 | 0 | 0 | 100 | 0.009 |
| Stenotopic species | | | | | | |
| <i>Cicadula quadrinotata</i> | 0 | 38 | 26 | 19 | 9 | 0.353 |
| <i>Euconomelus lepidus</i> | 0 | 50 | 0 | 0 | 0 | 0.051 |
| <i>Notus flavipennis</i> | 0 | 17 | 25 | 15 | 25 | 0.846 |
| <i>Forcipata citrinella</i> | 0 | 17 | 7 | 0 | 29 | 0.503 |
| <i>Macrostes septemnotatus</i> | 0 | 0 | 2 | 0 | 80 | 0.019 |
| <i>Sorhoanus assimilis</i> | 0 | 0 | 0 | 0 | 100 | 0.009 |

*Has been revised since our identification (Tishechkin 1998, see also Nickel 2003).

diversity in grasslands. Although it is clear that, in the long run, mowing is essential for preventing tree growth and succession, each single cutting event removes food resources and deposited eggs as well as shelter from sun, predators and other adverse forces (Curry 1994). In our study we found a distinct change correlated with mowing frequency, which, in terms of total number of species and of specialized and therefore often endangered species, was particularly noteworthy between single- and double-cut plots (see Figure 1, Table Appendix). This result could be confirmed on numerous meadow plots all over central Europe (Nickel and Ahtziger 1999) and on experimental plots studied by Morris (1981a). The latter author further studied the influence of the timing of mowing and found that the negative effects of a single July cut were almost as severe as two cuts in May and July.

Thus we conclude that the second annual cut exerts the most negative impact on above-ground insect communities and in the long term excludes

numerous insects, either by preventing them from successfully ovipositing, developing, or by severely deteriorating their favoured microclimatic conditions. This result poses a dilemma for conservation strategies that are mainly based on floristic evidence. Nickel and Hildebrandt (2003) found that floristically rich meadows, which were double cut in order to export nitrogen, were only poor in insect diversity. Moreover, these plots lacked most endangered species which occurred on nearby pastures and fallows. In general such conflicts should be solved by carefully balancing the conservation priorities and needs for each group and by installing a mosaic of different management regimes.

Efficiency of land use extensification for conservation and restoration of insect communities

Figure 3 demonstrates a general change of the insect fauna with decreasing land use intensity

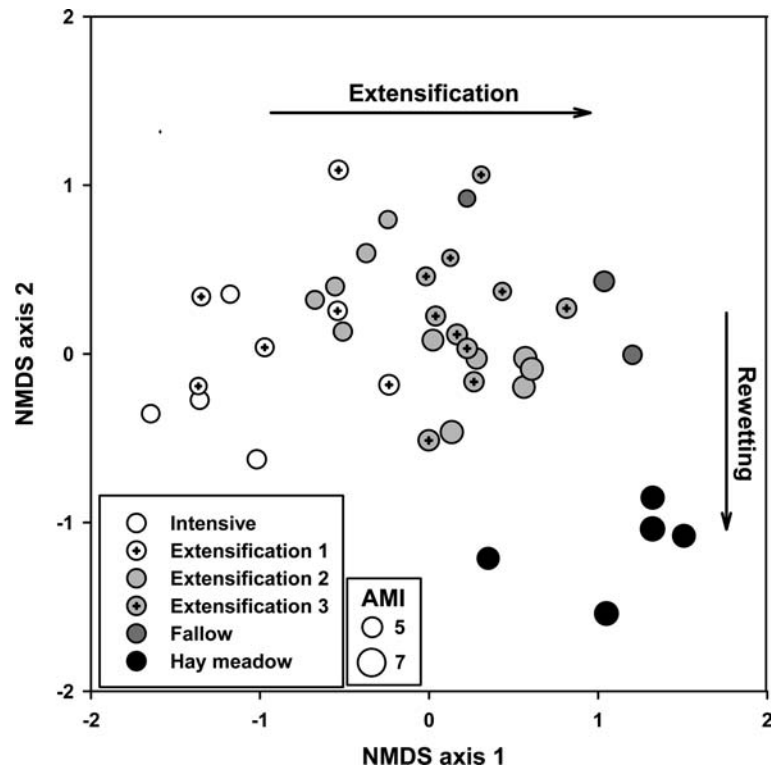


Figure 3. NMDS ordination of leafhopper communities of the Wiesmet floodplain (data from 1995 and 1996); each point represents the community of a single plot (Kruskal's stress = 0,29); circle sizes indicate the average values of Auchenorrhyncha moisture index (AMI) of all recorded species per plot.

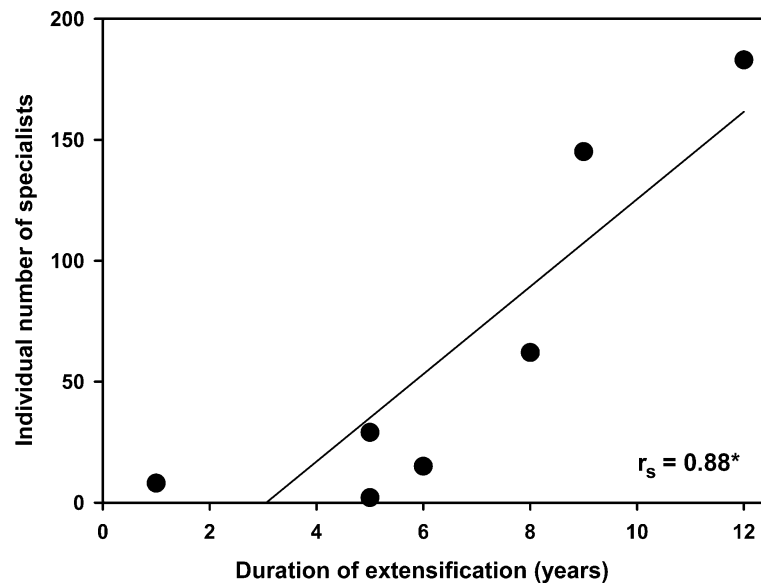


Figure 4. Individual numbers of specialists (oligotopic and stenotopic species) per plot versus the duration of extensification (contract duration) on extensification level 2 (E2) plots ($n = 7$, Wiesmet 1995). r_s = Spearman rank correlation.

along axis 1, and there is wide agreement that this relationship is causal (see above). However, in our plots a change is only visible along axis 1, but not along axis 2, and there appears to be no further convergence between communities of extensified and wet hay meadows, indicating that leafhopper communities in extensified plots do not develop towards their original composition before land drainage as represented by hay meadow remnants.

There are two possible explanations. First, the time span may not have been long enough to allow recolonisation. This idea does not seem plausible since most leafhoppers are easily transported by air currents or are good flyers and colonisers by themselves (Waloff 1973; della Giustina and Balasse 1999; Nickel 2003). Moreover, species numbers have actually increased in our extensified plots (Figure 1), and therefore, substantial immigration must have taken place. But the new invaders were not the typical hay meadow species, which largely remained confined to non-contract control plots. The second possible explanation, which we consider to be more likely, is a failure of the extensification program in restoring proper moisture conditions crucial for many hay meadow species. In order to prove this hypothesis we calculated an average Auchenorrhyncha moisture index (AMI) as a surrogate of soil moisture for which we did not have direct data (see section 3). As can be seen in the high AMI values in Figure 3, most typical hay meadow species show higher moisture requirements. A further argument is also that hostplants of most of these species (particularly *Carex* spp.) were absent from the extensified plots. Sanderson et al. (1995) also found that, besides plant composition, soil moisture was the important factor for the distribution of leafhopper communities in north-eastern England.

Our conclusion is that the extensification program resulted in a diversification of insect communities, but not “back” towards conditions pertaining before major drainage measurements were taken. Therefore, if we define the restoration of typical hay meadow communities as a conservation target, the program must be considered as insufficient, and further measures must be taken, notably a reversal of former drainage. Such unsatisfying results were also found in a similar agri-environmental program for the conservation of grassland birds through extensification of land

use run in the Netherlands (Kleijn et al. 2001, 2004).

The fact that the original communities are still far from being re-established even after 12 years of extensification raises the principal question as to whether this is possible at all. From the significant correlation between contract duration and specialist diversity in our E2 plots (Figure 4) we suggest that it takes about 5–10 years until the noticeable onset of community restoration, provided fertilising has been stopped. However, as seen above, the immigration of specialists does not necessarily imply that formerly lost species will return. Instead, there may be a shift towards more mesophilic or xerophilic communities, if original moisture conditions have not been restored. Principally we argue that an approximation to former hay meadow communities should be possible, based on the high dispersal and colonising ability even of predominantly brachypterous specialists (e.g. Morris 1990; Hollier et al. 1994; Achtziger 1997; Nickel 2003). In fact reproducing populations of many specialists are frequently found in relatively young habitats such as mining areas, abandoned fields and river banks subject to natural succession (Hahn 1996; Funke and Witsack 1998; Nickel 1999). However, it is not known how much time is necessary for what can be regarded as successful restoration of a hay meadow community. According to our results it would be a matter of decades.

As a possible way to accelerate the slow reestablishment of original communities, plant conservationists have successfully started to practice topsoil removal and subsequent import of mown plant material from species-rich sources (Tallowin and Smith 2001; Hölzel and Otte 2003). This approach has not yet been tested for its effects on invertebrates, but it may prove to be equally successful if transfer of mown material is repeated several times in order to allow emerging insect nymphs to feed on germinated plants.

The succession of recolonising leafhopper species in response to extensification

We assume that the higher species diversity in our extensified plots is actually due to recolonisation, but not to survival of small remnant populations,

although our two-year study design did not allow us to confirm this. There is, however, ample evidence from numerous other studies that many leafhopper species are capable of quickly and successfully immigrating into new and suitable habitats (see above). Moreover, depending on land use intensity and moisture there appears to be a more or less constant succession starting with pioneers which are followed by eurytopic, oligotopic and stenotopic species. Based on our data we propose an ecogram (*sensu* Ellenberg 1996) of extensification, which illustrates the relationship between the occurrence of grassland leafhoppers, land use intensity and moisture (Figure 5). At least for central European meadows it can be used as a predictive tool for extensification and as an indicator of restoration progress and success.

Our ecogram is based on the results of the present study as well as all available field data of central European grassland leafhoppers (e.g. Marchand 1953; Remane 1958; Emmrich 1966; Schiemenz 1969; Andrzejewska 1971; Nikusch 1976; Hildebrandt 1995; Achtziger and Nickel 1997; Niedringhaus 1997; Walter 1998; Achtziger et al. 1999; Nickel and Achtziger 1999; Bornholdt 2002; Nickel 2003; Nickel and Hildebrandt 2003; Nickel and Achtziger, unpublished data).

We arranged the species along a gradient of land use intensity from 'very intensive' to 'extensive' and 'not used' on the horizontal axis, and along a moisture gradient from 'very dry' to 'very wet' on the vertical axis. These arrangements were either supported by calculated indices from this study (Table 4) or were made tentatively where exact land use data were lacking, or from a combination of both. Therefore, the extensification ecogram must be read from left to right (i.e. the tail of the arrow marks the maximum tolerance of land use intensity, and the conditions for the species generally improve from here rightward, though they may deteriorate after having reached an optimum at intermediate intensity) and from top to bottom in response to rewetting measures (note that the position of the arrow indicates the tentative level of mean moisture requirements, but not their minimum). Altogether successful extensification should cause a rightward shift in community composition and a downward shift, where rewetting is involved (analogous to Figure 3).

Recommendations for the conservation and restoration of wet grassland

If we define generally high diversity and enhanced populations of endangered species as an appropriate conservation target, it appears clear that fertilising and mowing must be reduced. The precise question for the proper mowing regime, however, may pose a dilemma. On the one hand cessation would lead to reforestation and, as a consequence, to a total loss of grassland species within a few decades. Further, the removal of plant biomass leads to an extraction of soil nutrients which in turn favours plant diversity (see Rajaniemi 2002). Therefore, from an insect conservationist's point of view, grassland management should include as few treatments as possible, but also as many as necessary for reducing nutrient content and preventing growth of trees and shrubs. On the other hand each cut causes high mortality in most insect species, and many are even excluded in the long term through a second annual cut. In general only a single annual cut should be made, although a second cut may be advisable where nutrient content of soils is high. Cutting height should not be less than 10 cm. Fallow patches or strips rotationally mown only every few years should be retained in order to allow survival of specialists feeding on tall grasses, e.g. reed (*Phragmites australis*), reed-grass (*Phalaris arundinacea*) or small-reed (*Calamagrostis* spp.), many of which are hosts to species-rich guilds (Nickel 2003).

Our data also provide evidence for the importance of the original moisture conditions. In former fenland habitats, which have been artificially drained, recovery of original insect communities will remain fragmentary or simply inadequate if xerophilic species invade. We stress the role of original undrained hay meadows not only for conservation but also for the potential of recolonisation of extensified or set-aside patches. Their leafhopper species numbers were up to 28 in the Wiesmet floodplain (recorded only during two sampling occasions) and over 40 elsewhere in central Europe (Nickel, unpublished data). In many agricultural landscapes they nowadays provide the last refuges for specialists, and their proportion of endangered species is often high. According to our data sets their restoration through extensification appears out of reach even after 12 years of contract duration. Therefore

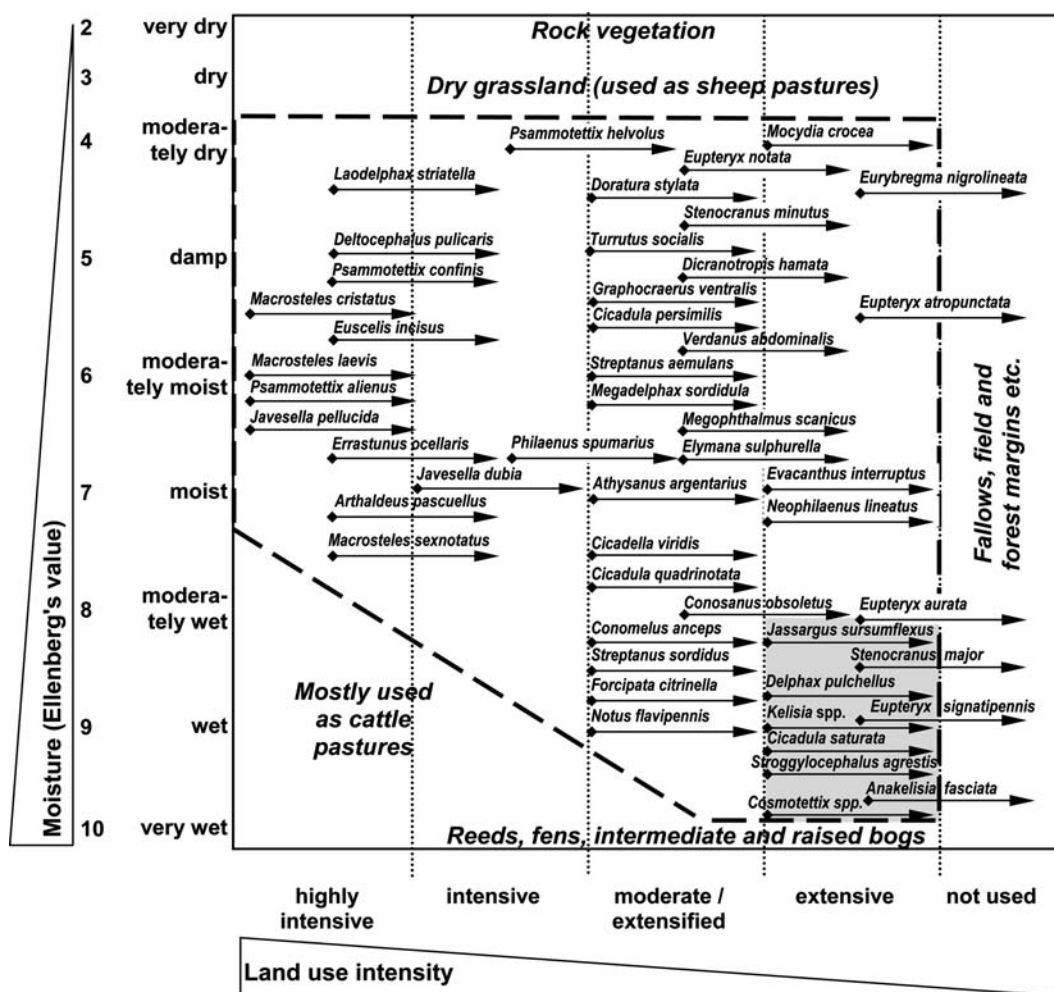


Figure 5. Ecogram of leafhopper species in meadows of central Europe. Species were arranged according to their moisture preferences (arrow at level of tentative median – see Nickel and Aichtziger 1999) and tolerance of land use intensity (tail of arrow indicates maximum tolerance of land use intensity, i.e. the species occurs from here rightwards). For reasons of space not all hygrophilic species are shown. Dashed lines indicate limits of grassland use as meadows, i.e. through frequent mowing; vertical dotted lines delimit land use intensity levels; the shaded area indicates the position of hay meadows.

conservation of existing patches should always have maximum priority. In addition to the preservation of single habitat patches, restoration strategies must be supplemented by a reversal of former drainage programs in order to raise ground-water levels, and by minimising habitat fragmentation and isolation on the landscape level (Kleijn et al. 2004; Tschardt and Brandl 2004).

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