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Effects of habitat management on vegetation and above-ground nesting bees and wasps of orchard meadows in Central Europe

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Abstract. We studied the vegetation, stand structure and communities of above-ground nesting bees and wasps in 45 orchard meadows that were grazed, mown or abandoned (15 of each) in an agricultural landscape near Göttingen, Germany. Total species richness of plants was significantly lower and the proportion of dead wood was significantly higher on abandoned meadows compared to mown or grazed meadows. Species richness of bees, eumenid wasps and sphecid wasps did not differ between the three management types. Abundance of sphecid wasps was significantly higher on abandoned than on managed orchard meadows. Landscape context did not affect management type. The results suggest that management practises affect vegetation more significantly than the studied insect groups.

Introduction

In many parts of the world man-made semi-natural habitats are the most species-rich remaining habitat types after the destruction of natural habitats (Pimentel et al. 1992). Especially in Central Europe, the cultural landscape greatly profits from patchily distributed semi-natural habitats (Tscharntke et al. 2002). These habitat types were created by extensive land use, e.g. grazing or mowing, and still are dependent on management to preserve their characteristic flora and fauna (Fry 1991). However, the intensification of agricultural land use and economic constraints have resulted in large-scale destruction of semi-natural habitats such as extensive grasslands, calcareous grasslands and orchard meadows (Baur and Erhardt 1995). Destruction of typical vegetation takes place by fertilisation, ploughing, reforestation, or secondary succession due to the absence of adequate management (Ausden and Treweek 1995; Balmer and Erhardt 2000).

The aim of grassland management is usually to increase economic productivity (Curry 1994), but for semi-natural habitats the focus of management is more and more on the conservation of species richness and biotic interactions (Sutherland and Hill 1995; Bignal and McCracken 1996; Pykälä 2000; Steffan-Dewenter and Tscharntke 2002).

Management by grazing or mowing is known to alter the botanical composition and structure of grassland vegetation (Morris 2000). Intermediate levels of disturbance are assumed to increase plant species richness and to reduce the dominance of competitive species (Curry 1994). Effects on insect communities are less well studied and existing results differ between species groups. Management may affect insects indirectly by altering the extent and quality of food supply, e.g. flowering plants, or directly by destroying the occupied vegetation (Morris 1967; Völkl et al. 1993). Grazing by animals is selective and results in higher sward heterogeneity compared to unselective mowing. Normally it takes place over a longer period of time, thereby constantly reducing the availability of inflorescences of flowering plants to a lower level. In contrast, the intervals between successive defoliation by mowing are longer and inflorescences of flowering plants are more abundant (Curry 1994). However, mowing temporarily leads to a complete reduction in inflorescences, and hence may have serious impacts on flower-visiting insects.

Extensive orchard meadows are a typical part of the cultural landscape in Central Europe and greatly differ from intensive fruit plantations. They are characterised by a species-rich herbaceous vegetation and old, tall fruit trees. Due to their extensive habitat management and high structural diversity, orchard meadows are one of the most diverse habitat types in Central Europe (Kornprobst 1994; Bünger and Kölbach 1995). Bees and wasps are characteristic species groups of orchard meadows. Particularly above-ground nesting species use nest holes made in dead wood by wood-boring insects and therefore depend on old fruit trees. As pollinators and predators, both bees and wasps are important functional groups of terrestrial ecosystems (LaSalle and Gauld 1993). They are useful indicators because bees reflect floral and wasps insect and spider diversity (Tscharntke et al. 1998). With 52% of the native bee fauna of Germany now in the regional Red Data Book of endangered species (Westrich et al. 1998), there is a growing urgency to understand the conservation needs of these ecologically important insects.

During recent decades the area of orchard meadows has been reduced by 80% due to intensified agricultural land use in Germany (Bünger and Kölbach 1995). Furthermore, many meadows are abandoned because farmers have ceased management activities as a result of their greatly reduced economic importance (Herzog and Oetmann 1997). The management decisions of land owners may depend on the landscape context within which the orchard meadows are placed, but concrete data are lacking.

Here, we studied the vegetation, stand structure and communities of trap-nesting bees and wasps in 45 orchard meadows that were grazed, mown or left fallow focusing on the following questions:

1. How does habitat management affect species richness and composition of vegetation?
2. How does habitat management affect the stand structure of fruit trees?
3. How does habitat management affect species richness and abundance of bees and wasps and parasitism by natural enemies?
4. Does habitat management depend on the surrounding landscape context?

Material and methods

Study region and study sites

The study was conducted in 1998 and 1999 in an agricultural landscape in southern Lower Saxony, Germany. On the basis of a complete mapping of orchard meadows in the study region, which covered 743 habitat fragments (Untere Naturschutzbehörde Göttingen, unpublished data), 45 orchard meadows were selected. These study sites ranged in size between 0.08 and 5.8 ha and represented three different management regimes: 15 meadows were regularly mown once or twice a year, 15 were grazed, usually by sheep, and 15 meadows were fallow, i.e. no management took place for at least 5 years. For each management type the study sites included all size classes from very small up to very large. To our knowledge no pesticides were used in any of the study sites.

Vegetation and tree stand structure

The floristic composition of herbs, grasses, and shrubs was recorded between the beginning of June and the end of July 1998 on a central plot of 25 m^2 in each study site. This area has been suggested as sufficient for perennial grassland vegetation (Dierschke 1994). However, it did not account for spatial heterogeneity of the larger study sites. Percent cover of each plant species, total cover of vegetation and mean plant height were recorded. Nomenclature follows Rothmaler et al. (1991) and Red Data list species Jedicke (1997).

To quantify stand structure in each study site the species of each tree were recorded, the perimeter at 1 m height (P) was measured and the proportion of dead wood was estimated by eye. Tree height (H) was estimated as $H = 0.49 \times P^{0.626}$ (1) and wood volume (V) per tree as $V = H \times B$ (2), where B is the tree base area $B = P^2/4\Pi$ (3). Inserting (1) and (3) in (2) results in $V = 0.49 \times P^{0.626} \times P^2/4\Pi$ (Kramer and Alparslan 1995). For each tree the volume of dead wood was calculated as wood volume (V)* proportion of dead wood. The sum for all trees represents the total volume of wood and dead wood for each study site, respectively.

Landscape composition

To analyse the spatial arrangement of orchard meadows and possible effects of landscape structure, a digital database was established using a geographical information system (GIS). The database included the locations of all orchard meadows and calcareous grasslands as the two most important semi-natural habitat types in the study region. Additionally, landscape composition was quantified by using digital thematic maps which allowed for the separation of semi-natural habitats (grassland, hedgerows, garden land), and of forests, arable land, settled area, and water area.

Insect communities

To analyse the response of insect communities to different management regimes, bees and wasps in trap nests were used as an indicator system (Tscharntke et al. 1998). On each of the 45 study sites three wooden posts (1.5 m height, 5–7 cm diameter), each with four nesting traps (i.e. a total of 540), were set up at regular distances during the growing period from April to September in 1998 and 1999. The nesting traps consisted of 150–180, 20 cm long common reed (*Phragmites australis*) internodes, which were put into plastic tubes of 10.5 cm diameter. In both study years, all nesting traps were sampled at the end of September and stored at 4 °C. In the laboratory, all reed internodes with nests of bees or wasps were taken out of the containers and opened with a scalpel. This allowed for the identification of the insect genus and in some cases of the species (see Gathmann and Tscharntke 1999). In most cases natural enemies (parasitoids and parasites of stored food) could also be easily identified. For each nest, the number of intact brood cells, the number of parasitised brood cells and the identifiable taxonomic level for hosts (bees or wasps) and natural enemies were recorded. To restrict the number of killed insects, only 10% of the intact brood cells of each species group were taken out of the nests and reared in the laboratory for species identification. The remaining nests with intact brood cells were put out in separate emergence boxes to the same study sites from which they had been removed.

Statistical analysis

The statistical analyses of the data were performed using Statgraphics plus for Windows 3.0 (Statgraphics 1997). As necessary, logarithmic or square-root transformation of variables was used to achieve normality. The arcsine-square root of P was used for proportions (Sokal and Rohlf 1995).

The effects of management on vegetation of orchard meadows were studied by using species richness and percent cover of all plants, and species richness and percent cover of grasses, herbs and shrubs. Stand structure was analysed using total wood volume, volume of dead wood, percentage of dead wood and tree density. For insect communities, we used total species richness (the sum of species found in 1998 and 1999 per study site) and abundance (the sum of brood cells found in 1998 and 1999 per study site) and species richness and abundance of separate insect groups (bees, sphecid wasps, eumenid wasps, natural enemies). The effect of landscape context on management regimes was analysed by using the proportion of orchard meadows and the total proportion of semi-natural habitats within eight circles of radius 250–3000 m around each study site. The area of the central study sites was not included in the calculation of these proportions.

Multifactor ANOVA was used with type of management as the main factor and habitat area as cofactor. Habitat area was included because of its great variability within each management type and the known effect of area on species richness and abundance (Steffan-Dewenter and Tscharntke 2000). F-statistics and P-values for Type III sums of squares are reported. To determine which means are significantly different from which other means, Tukey's honestly significant difference (HSD) procedure was used at the 95% level. Arithmetic means and standard errors are given in the text.

Results

Vegetation

Altogether 154 plant species were identified in the 45 study sites, comprising 29 grass species, 112 herb species and 13 shrub species. The plant species with the highest constancy were *Dactylis glomerata*, occurring in 41 plots, *Anthriscus sylvestris* (35 plots), *Arrhenatherum elatius* (34 plots) and *Urtica dioica* (31 plots). The species with the highest mean cover over all study sites were the grasses *Arrhenatherum elatius* (20.1%), *Poa trivialis* (12.1%), *Dactylis glomerata* (11.4%), *Holcus lanatus* (8.4%), and *Festuca rubra* (7.7%). Eleven of the recorded plant species (7.1%) are endangered according to the Red Data list for Lower Saxony (e.g. *Primula veris*, *Tragopogon pratensis*, *Avenochloa pratensis*, *Agrimonia eupatoria*, *Peucedanum ostruthium*, and *Carex flacca*). The mean number of species per study site on a 25 m^2 plot was 21.5 ± 7.1 for all species, 13.6 ± 5.2 for herb species, 7.1 ± 2.5 for grass species and less than one species for shrubs.

Habitat management had significant effects on total species richness of plants and community composition (Appendix 1). The highest number of plant species was found on mown meadows and the lowest on abandoned meadows. Species richness of grazed meadows was intermediate (Figure 1A, Table 1). Analysing herbs and grasses separately, these effects remained significant only for grasses but not for herbs (Figure 1B and C). The mean plant height was significantly affected by management type ($F = 6.71$, $n = 45$, $P = 0.003$) and was highest on abandoned meadows (99.7 ± 7.8 cm), intermediate on mown meadows (84.7 ± 11.1 cm), and lowest on grazed meadows (55.0 ± 7.0 cm). Neither the total cover of vegetation nor the percent cover of herbs, grasses or shrubs showed significant differences between management types (results not shown).

Stand structure

Dominant fruit tree species on orchard meadows were apples (*Malus domestica*, 50.3 ± 5.1%), sweet cherries (*Prunus avium*, 27.6 ± 5.5%), plums (*Prunus domestica*, 12.3 ± 2.7%), pears (*Pyrus communis*, 5.5 ± 1.1%), and sour cherries (*Prunus cerasus*, 3.4 ± 1.3%). The proportion of different fruit tree species did not significantly differ between the three management types, but varied greatly within each type.

The total wood volume per m^2, the volume of dead wood per m^2 and the tree density did not show significant responses to management (Table 1). Only the percentage of dead wood was higher on abandoned orchard meadows compared to grazed or mown meadows (Figure 2).

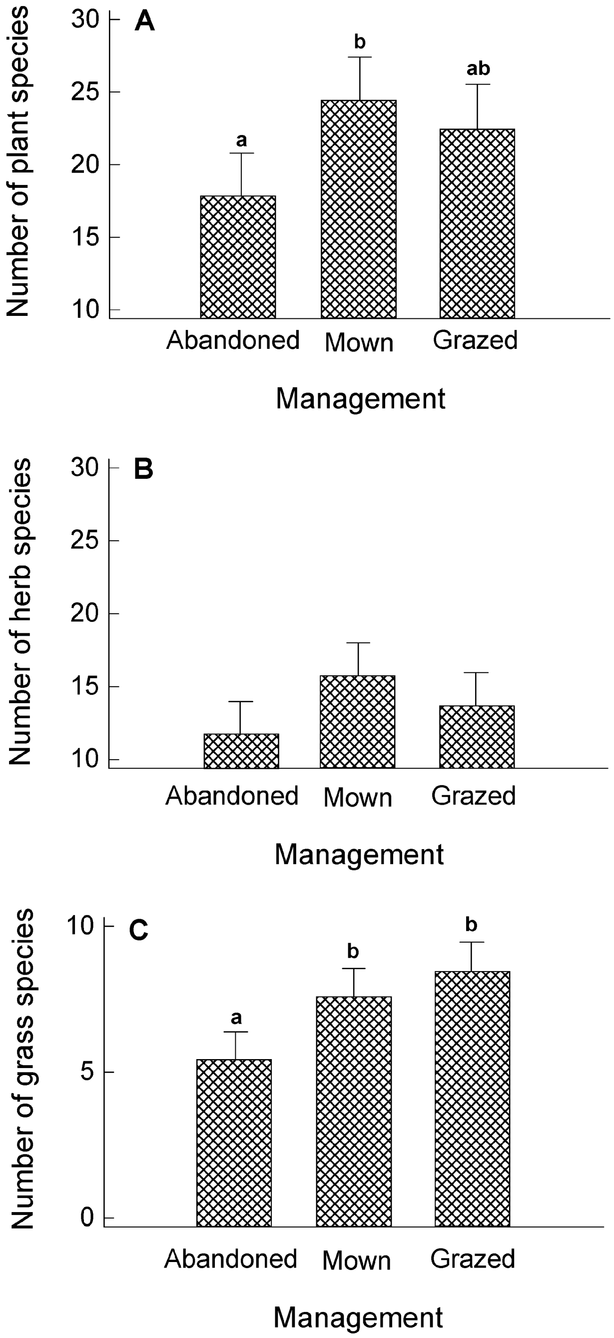

Figure 1. Effects of management type on vegetation of orchard meadows: (A) number of plant species per 25 m^2; (B) number of herb species per 25 m^2; (C) number of grass species per 25 m^2. Arithmetic means and Tukey intervals are given. Significantly different groups are shown by different letters. For statistics see Table 1.

Table 1. Effects of habitat management on vegetation and stand structure of 45 orchard meadows.

Dependent variable	Main factor (management)		Cofactor (area)	
	F-value	*P*-value	*F*-value	*P*-value
Number of plant species	3.79	0.031	0.00	0.964
Number of herb species	2.24	0.119	0.19	0.668
Number of grass species	6.69	0.003	1.01	0.319
Log wood volume/m^2	1.48	0.234	6.65	0.014
Log dead wood volume/m^2	1.69	0.197	3.75	0.059
arcsin$\sqrt{}$ proportion of dead wood	3.37	0.044	0.03	0.872
Fruit trees/m^2	0.26	0.770	5.19	0.028

Results of Multifactor ANOVA are given.

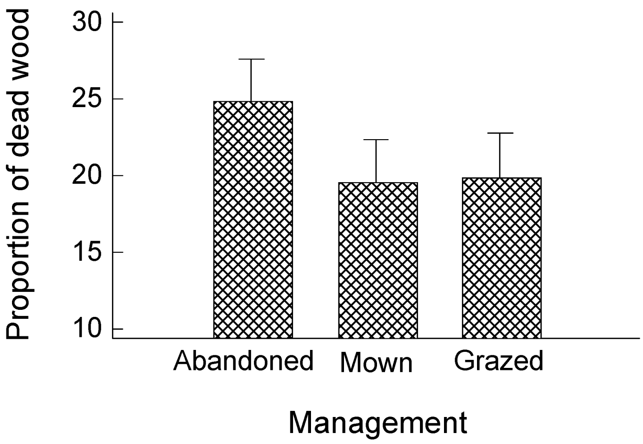

Figure 2. Effects of management type on the proportion of dead wood (arcsin$\sqrt{p}$). Arithmetic means and Tukey intervals are given. For statistics see Table 1.

Bees, wasps, and natural enemies

In the two study years, 30700 brood cells were analysed comprising 17278 brood cells of 13 solitary bee species (Apidae), 8701 brood cells of 12 eumenid wasp species (Eumenidae), 5491 brood cells of 13 sphecid wasp species (Sphecidae) and 253 brood cells of 2 spider wasp species (Pompilidae) (Appendix 2).

Neither the number of species nor the number of brood cells showed significant differences for all species, or separately for bees, eumenid or sphecid wasps between the three management types (Table 2). Only the abundance of sphecid wasps was significantly higher on abandoned orchard meadows compared to grazed or mown meadows (Figure 3). Twenty-six species of natural enemies from nine different families attacked 5401 brood cells (16.9%) of bees and wasps (Appendix 2). However, no significant differences between the three management types existed for the species richness of natural enemies and the rate of parasitism of bees and wasps (Table 2).

Table 2. Effects of habitat management on species richness and abundance of trap-nesting bees, wasps and their natural enemies ($n = 45$ orchard meadows).

Dependent variable	Main factor (management)		Cofactor (area)	
	F-value	*P*-value	*F*-value	*P*-value
Species number of bees and wasps	1.35	0.270	12.71	0.0009
Species number of bees	1.52	0.231	12.21	0.001
Species number of eumenid wasps	0.12	0.891	6.23	0.017
Species number of sphecid wasps	1.45	0.247	2.71	0.107
Species number of natural enemies	0.13	0.882	9.27	0.004
Number of brood cells of bees and wasps[a]	0.01	0.994	3.23	0.080
Number of brood cells of bees[a]	1.45	0.246	4.98.	0.031
Number of brood cells of eumenid wasps[a]	0.41	0.669	3.40	0.073
Number of brood cells of sphecid wasps[a]	5.88	0.006	0.02	0.899
Percentage of parasitism of brood cells of bees and wasps[b]	2.20	0.123	0.04	0.843
Percentage of parasitism of brood cells of bees[b]	1.92	0.159	0.36	0.550
Percentage of parasitism of brood cells of eumenid wasps[b]	1.24	0.298	0.12	0.732
Percentage of parasitism of brood cells of sphecid wasps[b]	1.87	0.167	1.62	0.211

Results of Multifactor ANOVA are given. [a]Square-root transformed data were used. [b]Data were $\arcsin\sqrt{p}$ transformed.

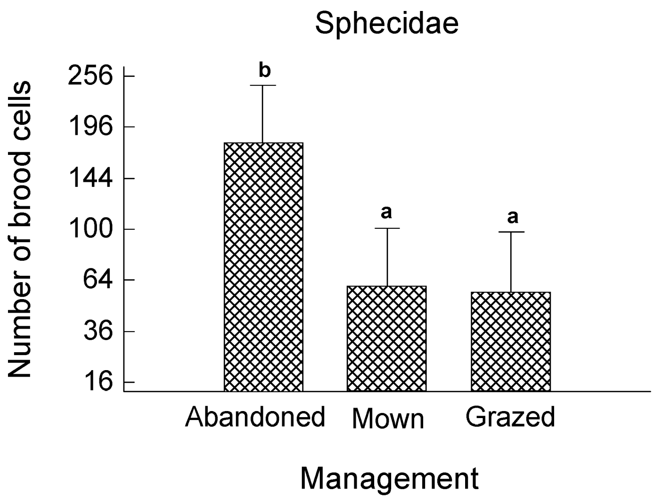

Figure 3. Effects of management type on the abundance of sphecid wasps. Arithmetic means and Tukey intervals are given. For statistics see Table 2.

Landscape context

The mean percentage of orchard meadow area in the study region was 0.26%. Orchard meadows were not randomly distributed but were spatially aggregated: the proportion of orchard meadows in the surrounding landscape was significantly higher for small circles of 250 m radius than for larger circles (Figure 4). A very similar pattern existed for the total proportion of semi-natural habitats. Its propor-

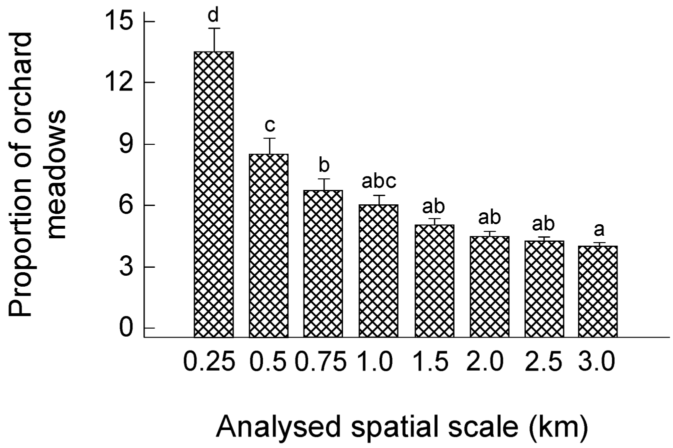

Figure 4. Proportion (percent area) of orchard meadows (arcsin$\sqrt{p}$, back-transformed values are shown in the figure) in the surrounding landscape at eight different spatial scales. Arithmetic means and Tukey intervals are given. $F = 28.6$, $P < 0.001$, $n = 360$.

tion was significantly higher in the close neighbourhood of orchard meadows compared to the average proportion of semi-natural habitats in the study region.

Furthermore, the proportion of orchard meadows in the surrounding landscape significantly increased with the size of the central study site (arsin$\sqrt{y} = -22.6 + 9.6 \log10x$, $r = 0.485$, $P = 0.0009$), indicating that larger orchard meadows were better connected with other habitat fragments than smaller meadows. The distribution of mown, grazed or abandoned meadows was not affected by landscape context, i.e. the proportion of semi-natural habitats or the diversity of habitat types in the surrounding landscape.

Discussion

In this study, we analysed the vegetation, stand structure and insect communities in orchard meadows that were mown, grazed or left fallow. The strongest effects of different management types were found for the species richness of plants, which was significantly lower after abandonment of orchard meadows. This result corresponds to earlier studies showing similar effects on plant diversity for other habitat types (Erhardt 1985; Linusson et al. 1998; Morris 2000). Our results suggest that grazing mainly promoted species richness of grasses, whereas mowing increased species richness of herbs. Generally, grasses are more tolerant to grazing than herbs because of the protected location of meristematic zones near the ground (Tscharntke and Greiler 1995).

Many local studies describe the high species richness of orchard meadows (Kornprobst 1994; Bünger and Kölbach 1995). Similarly, the 40 species of bees and wasps found in our study is a very high number as compared to studies of above-ground nesting bees and wasps in other habitat types (Gathmann 1998). The high species richness of orchard meadows is presumably a consequence of the floristic diversity, which seems to be enhanced by extensive management, and the structural complexity due to vertical stratification.

The effects of grazing, mowing or abandoning of orchard meadows on insect communities were less significant. Only the abundance of sphecid wasps significantly increased on abandoned meadows. The unexpectedly weak effects of management may be explained by two points: in contrast to herbivorous insects, bees and wasps depend only indirectly on the vegetation layer for food supply. Bees need flowering plants for collecting nectar and pollen and wasps search for larvae of herbivorous insects, but also for spiders and aphids (Gathmann and Tscharntke 1999). Furthermore, flowering fruit trees are additional important food sources for bees, and larvae of codling moth (Tortricidae) on apple trees are often used by eumenid wasps for provisioning of brood cells (Harris 1994; own observations). Therefore, changes in the herbaceous vegetation may be less significant for the studied insect groups than for species which directly inhabit the vegetation layer.

Second, grazing, mowing or abandoning may have opposing effects on habitat quality in terms of food resources and nesting places. For example, abandonment of orchard meadows leads to a decrease in plant species richness and the dominance of a few competitive species, thereby possibly reducing the availability of flowering herbaceous plants. On the other hand, due to the absence of tree cutting, the proportion of dry, dead wood, and thereby the availability of nesting holes, was presumably higher on abandoned meadows. This could be the reason for the increased abundance of sphecid wasps on abandoned orchard meadows. Other studies support the view that species occupying the vegetation are likely to be more markedly affected than above-ground nesting bees and wasps, but also indicate that positive or negative effects of management can be found depending on the species biology (Curry 1994; Balmer and Erhardt 2000; Steffan-Dewenter and Tscharntke 2002). For example, some species of leafhoppers and grasshoppers (Andrzejewska 1979) as well as some butterfly species (Thomas 1991) were favoured by management, whereas total species richness of butterflies, including many endangered species, was significantly higher on old fallows than on extensively grazed or mown calcareous grasslands (Balmer and Erhardt 2000). However, long-term abandonment results in a significantly reduced species richness of both vegetation and butterflies (Erhardt 1985). For orchard meadows we are only aware of very few other studies on the effects of management. In a comparison of epigaeic Coleoptera assemblages in organic, conventional, and abandoned orchards in Canada, abandoned orchards displayed the greatest diversity of non-predaceous beetles, but abundance of predaceous beetles was highest in conventional orchards (Pearsall and Walde 1995).

Although some species groups may temporarily profit from abandonment, the characteristic vegetation and insect communities of semi-natural, man-made habitats like orchard meadows depend on extensive mowing or grazing. Furthermore, there is a need for new planting to replace old and dying fruit trees (Niemeyer-Lüllwitz 1993). Recent conservation approaches in Germany try to increase the economic value of orchard meadows for landowners to ensure appropriate management (Kornprobst 1994). We did not find effects of landscape structure on management practice, but it should be stressed that orchard meadows (and other semi-natural habitats) are of special importance in intensively managed agricultural landscapes for the preservation of species richness and biotic interactions (Steffan-Dewenter et al. 2001). In the long term the exceptional value of this habitat type for nature conservation can only be preserved by adequate management.

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Appendix 1

Plant species on orchard meadows occupying five or more out of 45 study sites.

Plant species	Abandoned meadows ($n = 15$)		Mown meadows ($n = 15$)		Grazed meadows ($n = 15$)	
	Number of occupied habitats	Mean percent cover	Number of occupied habitats	Mean percent cover	Number of occupied habitats	Mean percent cover
Dactylis glomerata	14	8.07	14	18.87	13	7.27
Anthriscus sylvestris	11	3.77	12	1.43	12	1.28
Arrhenatherum elatius	11	25.03	15	27.30	7	8.50
Urtica dioica	12	7.27	9	1.07	10	2.03
Poa trivialis	4	5.67	13	12.67	11	18.00
Galium aparine	13	5.80	7	1.60	6	0.50
Cerastium holosteoides	3	0.20	11	1.00	12	1.27
Veronica chamaedrys	10	2.20	7	1.20	8	1.60
Poa pratensis	7	4.53	11	6.93	7	6.67
Taraxacum officinale	1	0.07	13	2.93	11	1.17
Holcus lanatus	8	7.93	5	3.33	10	14.07
Heracleum sphondylium	8	0.54	8	0.58	6	0.58
Trifolium repens	0	0.00	8	2.67	13	4.87
Festuca rubra	7	10.67	3	1.87	9	10.67
Galium mollugo	5	1.50	6	3.61	8	2.27
Glechoma hederacea	8	1.80	3	0.20	6	1.53
Bromus ramosus	0	0.00	7	1.00	10	1.27
Phleum pratense	2	0.13	8	0.80	7	0.47
Achillea millefolium	4	0.40	5	0.60	7	1.27
Festuca pratensis	2	0.13	5	0.73	9	1.40
Geum urbanum	8	1.27	4	0.23	3	0.13
Elymus repens	9	3.40	3	0.47	3	0.20

Appendix 1. (*Continued*)

Plant species	Abandoned meadows (*n* = 15)		Mown meadows (*n* = 15)		Grazed meadows (*n* = 15)	
	Number of occupied habitats	Mean percent cover	Number of occupied habitats	Mean percent cover	Number of occupied habitats	Mean percent cover
Lolium perenne	0	0.00	7	2.20	8	7.00
Alopecurus pratensis	3	0.33	5	0.57	6	4.40
Trisetum flavescens	3	0.80	6	2.00	5	0.93
Ranunculus acris	2	0.13	6	0.77	6	0.67
Convolvulus arvensis	2	0.13	7	0.40	4	0.37
Rumex acetosa	2	0.07	5	0.27	4	0.17
Plantago lanceolata	1	0.07	7	0.47	3	0.27
Agrostis stolonifera	4	5.33	2	1.67	4	2.80
Trifolium pratense	0	0.00	5	1.80	5	0.93
Vicia sepium	3	0.60	3	0.47	3	0.67
Cirsium arvense	5	1.67	1	0.03	3	0.17
Lamium album	4	0.27	3	0.27	2	0.07
Veronica arvensis	0	0.00	7	1.03	2	0.13
Galeopsis tetrahit	9	0.35	0	0.00	0	0.00
Hypericum perforatum	3	0.11	2	0.07	2	0.13
Crataegus spp.	2	0.07	2	0.13	3	0.13
Rosa spp.	0	0.00	5	0.38	2	0.10
Anthoxanthum odoratum	0	0.00	2	0.13	5	0.33
Crepis biennis	0	0.00	4	0.34	3	0.47
Pimpinella saxifraga	2	0.10	1	0.07	3	0.20
Bellis perennis	1	0.01	2	0.13	3	0.27
Rumex obtusifolius	2	0.10	2	0.10	2	0.04
Primula veris	2	0.13	4	0.41	0	0.00
Vicia tetrasperma	2	0.13	3	0.77	0	0.00
Viola hirta	1	0.07	3	0.20	1	0.07
Geranium molle	0	0.00	3	0.60	2	0.33
Stellaria media	0	0.00	3	0.17	2	0.40
Bromus sterilis	0	0.00	2	0.40	3	1.20
Cynosurus cristatus	0	0.00	0	0.00	5	2.20
Tragopogon pratensis	1	0.07	4	0.27	0	0.00
Rubus fruticosus agg.	4	2.53	1	0.03	0	0.00

The number of occupied habitats and the mean percent cover for abandoned, mown and grazed meadows is given.

Appendix 2

Community structure of trap-nesting bees, wasps and their natural enemies on 45 orchard meadows.

Family	Genus	Species	Number of brood cells	Colonised sites (of 45)	Percentage parasitised brood cells	Natural enemies
Apidae	*Osmia*	*rufa* (Linnaeus 1758)	14486	42	19.94	*Cacoxenus indagator*, *Monodontomerus obscurus*, *Anthrax anthrax*, *Megatoma undata*, Acari,
		leaiana (Kirby 1802)	126	8	9.52	*Megatoma undata*
		brevicornis (Fabricius 1798)	29	2	–	
		parietina (Curtis 1828)	13	1	53.39	*Megatoma undata*
		Caerulescens (Linneaus 1758)	1	1	–	
		spp.	124	5	10.48	*Cacoxenus indagator*
	Megachile	*lapponica* (Thomson 1872)	31	4	–	
		Versicolor (Smith 1844)	16	2	–	
		spp.	563	13	4.62	*Ephialtes manifestator*, *Megatoma undata*, *Melittobia acasta*
	Hylaeus	*communis* (Nylander 1852)	185	17	2.70	*Gasteruption assectator*, *Coelopencyrtus arenarius*, *Megatoma undata*
		difformis (Eversmann 1852)	5	1	–	
		spp.	1141	26	17.97	*Coelopencyrtus arenarius*, *Gasteruption assectator*, *Megatoma undata*
	Heriades	*truncorum* (Linnaeus 1758)	19	2	–	
		crenulatus (Nylander 1856)	10	2	–	
		spp.	129	13	12.9	*Ephialtes manifestator*, *Melittobia acasta*
	Chelostoma	*florisomne* (Linnaeus 1758)	59	8	28.8	*Ephialtes manifestator*, *Sapyga clavicornis*, *Melittobia acasta*
		spp.	338	15	4.44	*Ephialtes manifestator*, *Sapyga clavicornis*, *Megatoma undata*, Chrysididae
	Anthidium	*lituratum* (Panzer 1801)	1	1	–	
		spp.	2	1	–	
Eumenidae	*Symmorphus*	*bifasciatus* (Linnaeus 1761)	76	7	1.32	Chrysididae
		connexus (Curtis 1826)	54	2	–	
		crassicornis (Panzer 1798)	4	1	25.0	*Chrysis fulgida*
		debilitatus (Saussure)	11	2	–	
		gracilis (Brulle 1832)	9	2	–	
	Discoelius	*zonalis* (Panzer 1801)	1	1	–	
	Ancistrocerus	*antilope* (Panzer 1798)	165	15	0.7	Acari
		gazella (Panzer 1798)	32	4	9.38	*Ephialtes manifestator*

Appendix 2. (*Continued*)

Family	Genus	Species	Number of brood cells	Colonised sites (of 45)	Percentage parasitised brood cells	Natural enemies
		nigricornis (Curtis 1826)	53	7	7.55	Chrysididae, *Melittobia acasta*
		parietinus (Linnaeus 1761)	37	3	10.81	*Chrysis solida*
		trifasciatus (Müller 1776)	139	12	12.23	*Chrysis schencki*, *Chrysis angustula* spp. *Angustula*, *Ephialtes manifestator*
	Allodynerus	*rossii* (Lepeletier 1841)	6	2	–	
	gen.	spp.	8098	45	14.02	*Chrysis corusca*, *Chrysis cyanea*, *Chrysis fulgida*, *Chrysis ignita Spec A*, *Chrysis longula*, *Chrysis schencki*, *Chrysis solida*, *Chrysis angustula* spp. *Angustula*, *Ephialtes manifestator*, *Megatoma undata*, *Melittobia acasta*, Acari
Sphecidae	*Trypoxylon*	*attenuatum* (Smith 1851)	1	1	–	
		cf. medium (de Beaumont 1945)	3	1	–	
		clavicerum (Lepeletier & Serville 1825)	249	22	4.02	*Megatoma undata*
		figulus (Linnaeus 1758)	109	5	1.83	*Ephialtes manifestator*, Chrysididae
		minus (de Beaumont 1945)	98	12	11.20	*Chrysis cyanea*
		spp.	4073	41	20.43	*Chrysis cyanea*, *Ephialtes manifestator*, *Nematopodius debilis*, *Nematopodius formosus*, *Stenarella domator*, *Megatoma undata*, *Melittobia acasta*
	Spilomena	*troglodytes* (van der Linden 1829)	30	4	6.67	*Megatoma undata*, *Melittobia acasta*
	Rhopalum	*clavipes* (Linneaus1758)	16	3	–	
	Psenulus	*bevitarsis* (Merisuo 1937)	1	1	–	
		spp.	11	1	100	*Megatoma undata*
	Pemphredon	*lugens* (Dahlbom 1842)	4	1	–	
	Passaloecus	*corniger* (Shuckard 1837)	17	7	–	
		gracilis (Curtis 1834)	23	2	4.35	*Megatoma undata*
		insignis (van der Linden 1829)	131	8	12.98	*Lochetica westoni*, *Poemenia collaris*, *Poemenia hectica*, *Megatoma undata*
		spp.	673	33	12.78	*Omalus aeneus*, *Omalus auratus*, *Poemenia collaris*, *Megatoma undata*, *Melittobia acasta*
	Nitela	*spinolae* Latreille 1809	63	13	14.30	*Megatoma undata*
		spp.	5	2	–	
Pompilidae	*Dipogon*	*subintermedius* (Magretti 1886)	19	4	–	
	Dipogon	spp.	193	23	13.99	*Megatoma undata*, *Melittobia acasta*, Chrysididae
	Auplopus	*Carbonarius* (Scopli 1763)	36	3	–	
	gen.	spp.	5	3	60.0	*Megatoma undata*

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