

Succession of bee communities on fallows

Ingolf Steffan-Dewenter and Teja Tschardtke

Steffan-Dewenter, I. and Tschardtke, T. 2001. Succession of bee communities on fallows. – *Ecography* 24: 83–93.

Wild bee communities were studied on one- to five-year-old set-aside fields with naturally developed vegetation ($n = 20$), and old orchard meadows ($n = 4$) to analyse effects of secondary succession on species diversity, resource use and associated life history traits. General theory predicts a steady increase of species richness with age of succession. In contrast, we found a first maximum in species richness of bees on two-year-old set-aside fields and a second on old meadows. Successional changes of bee communities were related to changes of vegetation. The transition from pioneer successional stages, dominated by annuals, to early successional stages, dominated by perennials, resulted in the highest species richness of flowering plants in the second year within the first five years of succession. Species richness of flowering plants was the best predictor variable for species richness of bees, whereas the cover of flowering plants correlated with the abundance of bees. Annual plants were visited more often and perennials less often than expected from their flower cover. Halictidae tended to prefer flowers of annuals, whereas Megachilidae, Apidae and Anthophoridae significantly preferred perennials. In departure from successional theory, body size, proportion of specialised bees and proportion of parasitic bees did not significantly increase with successional age, but number of generations and the proportion of soil-nesting bees decreased with successional age. Comparison of different management types showed that set-aside fields with naturally developed vegetation supported much more specialised and endangered bee species than set-aside fields sown with *Phacelia tanacetifolia*.

I. Steffan-Dewenter (isteffa@gwdg.de) and T. Tschardtke, Dept of Agroecology, Univ. of Göttingen, Waldweg 26, D-37073 Göttingen, Germany.

Destruction of habitats and intensification of land use have resulted in the loss of species richness and abundance of wild bees (Hymenoptera: Apoidea) in many European regions (Westrich 1989, Osborne et al. 1991, Banaszak 1992, O'Toole 1993). Bees are essential for both managed and natural ecosystems as pollinators of cultivated and wild plants (Neff and Simpson 1993). The decline of bees may negatively affect seed set of wild plants and yields of crops requiring insect pollination (Corbet et al. 1991, Williams 1996, Steffan-Dewenter and Tschardtke 1999). In the long term, the loss of plant-pollinator interactions may alter terrestrial ecosystems (Allen-Wardell et al. 1998). The main reasons for the decline of wild bees are the loss of habitats with suitable nesting sites and diverse vegetation providing a temporal continuum of pollen and nectar

resources (O'Toole 1993). Bees mainly depend on extensively used man-made habitats. Therefore, changes in the agricultural landscape are of special importance for their conservation.

Since 1988 set-aside of farmland has been established as an instrument of the EU agricultural policy to restrict overproduction of crops. The scheme allows rotational set-aside for one year or non-rotational set-aside for five years. Fields can be sown, or natural regeneration of vegetation can be allowed (Stedmann 1994). Especially the sowing of *Phacelia tanacetifolia*, an important honey bee forage plant, has been promoted by beekeepers in Germany and other European countries (Bauer and Engels 1991, Williams and Carreck 1994). Despite its primarily economic motivation, set-aside opens new chances for nature conservation in

Accepted 21 March 2000

Copyright © ECOGRAPHY 2001

ISSN 0906-7590

Printed in Ireland – all rights reserved

the agricultural landscape (Corbet 1995, Tschardt et al. 1996). Effects of set-aside on wild bee communities can only be understood within the context of secondary succession.

Studies on secondary succession of plant communities have a long tradition, and extensive literature exists dealing with changes during early succession (e.g. Tramer 1975, Bazzaz 1975, 1996) and mechanisms of succession (e.g. Connell and Slatyer 1977, Huston and Smith 1987, Tilman 1990). Studies on changes of insect communities and plant-insect interactions during succession are less common. Generally, a linear increase in species richness with successional age is expected (Odum 1969, Brown and Southwood 1987). In the long term, overall arthropod diversity has been shown to increase during old field succession (Siemann et al. 1999), but patterns of species richness and abundance greatly differ in relation to the studied insect groups (e.g. Brown and Hyman 1986, Brown and Southwood 1987, Greiler 1994, Gathmann et al. 1994, Steffan-Dewenter and Tschardt 1997). Furthermore, depending on the used time scale, non-linear changes of species richness during succession may be clouded by the general long-term increase of species diversity. Short-term changes of insect communities can be expected during the first years of succession, when the plant communities rapidly change from annuals to perennials (Corbet 1995, Steffan-Dewenter and Tschardt 1997). General hypothesis predict and some empirical data show that changes in insect communities during succession are driven by vegetation structure and diversity (Brown and Southwood 1983, Brown 1985, Brown and Southwood 1987, Steffan-Dewenter and Tschardt 1997, Siemann et al. 1999). The interactions between the succession of plants and pollinating or herbivorous insects are of special interest (Parrish and Bazzaz 1979, Brown 1985). Species-poor bee communities in pioneer successional stages may lead to reduced seed set and may favour the selection of autogamous plants. Corbet (1995) expects that pioneer successional vegetation is less attractive for bumble bees because they prefer perennial plants with larger amounts of nectar (Fussell and Corbet 1992, Corbet et al. 1995). Parrish and Bazzaz (1979) found that annuals were visited more often by halictid bees and syrphid flies, whereas perennial prairie species were preferred by apid and megachilid bees.

Successional changes include changes of community structure and of associated life history traits from pioneer and early to mid successional stages (Grime 1977, Brown and Southwood 1987, Huston and Smith 1987, Tilman 1990, Corbet 1995). Arthropod body size, which is correlated with dispersal ability (e.g. Novotny 1994), decreased with successional age in some studies (Steffan-Dewenter and Tschardt 1997, Siemann et al. 1999), but in others not (e.g. Brown 1985). In early successional stages a bimodal distribution of body size may occur, comprising large active dispersers and small

passive dispersers (Corbet 1995). Niche specialisation and generation time are expected to increase with successional age (Odum 1969). Possible reasons for increased food plant specialisation are increased competition and therefore smaller niche breadth, a higher predictability of food resources in later successional stages and therefore a higher chance of specialised species to persist (Brown and Southwood 1983) or a qualitative instead of a quantitative anti-herbivore defence of plants in later successional stages resulting in more specialised herbivores (Edward-Jones and Brown 1993). Rapid reproduction and more generations per year may be of selective advantage in unpredictable early successional stages (Brown 1985, Hodgson 1993). The proportion of predators and parasitoids is expected to increase during succession enhancing predator-prey interactions (Brown and Southwood 1987). In conclusion, secondary succession can be studied on the level of 1) community structure and species diversity, 2) interactions between plants and insects and 3) life history traits. Here we analysed early successional bee communities on one- to five-year-old set-aside fields with naturally developed vegetation and mid-successional old orchard meadows to answer the following questions: 1) How does species richness, abundance and community structure of wild bees change with successional age? 2) How do successional changes of plant communities affect resource availability for bees? 3) Do life history traits of bees change in the hypothesised way during succession? 4) Are set-aside fields sown with *Phacelia tanacetifolia* less species-rich than set-aside fields with naturally developed vegetation?

Material and methods

Study region and study sites

The study was conducted in 1993 in Baden-Württemberg (southwest Germany) in an agricultural landscape named Kraichgau. The mean annual temperature is 9–9.5°C and mean annual rainfall is 700–800 mm (Hölzinger 1981). The suitable climatic and edaphic conditions resulted in early settlement and agricultural land use by man at the end of the Neolithic (Schottmüller 1961).

To establish a successional gradient we selected one- to five-year-old set-aside fields with natural regeneration of vegetation and – for comparison – one-year-old set-aside fields sown with *Phacelia tanacetifolia* and > 30 yr old orchard meadows, each with four replicates, i.e. 28 study sites altogether (Table 1). The fields were set-aside in autumn after the harvest of the last crops which were cereals in all cases. Set-aside fields were mown at the beginning of July, and orchard meadows once or twice between June and August. Mean field size was 0.6 ± 0.4 ha and did not signifi-

cantly differ between the seven field types (one-way ANOVA: $F_{6,21} = 0.81$, $n = 28$, $p = 0.57$). Habitat connectivity of the study fields was characterised by the percentage of the total border line of each field adjoining to semi-natural habitats like grasslands, orchard meadows, hedges, or old fallows. The sown *Phacelia* fields and the one- to five-year-old set-aside fields with naturally developed vegetation did not significantly differ in the proportion of adjoining semi-natural habitats ($F_{5,18} = 0.81$, $n = 24$, $p = 0.53$), whereas orchard meadows were significantly better connected to other semi-natural habitats ($F_{6,21} = 5.04$, $n = 28$, $p = 0.003$).

Vegetation and resource availability

Plant species composition, percent cover of each species and total cover of vegetation were mapped twice, in June and August, on a plot of 49 m² in the centre of each field. Additionally, five times between May and August, we recorded species composition of melittophilous flowering plants, and estimated percent flower cover of each species and total flower cover of all species on each field. Melittophilous plants are insect-pollinated species which provide nectar and/or pollen as attractants. For statistical analyses, we used arithmetic means of five observation times for each field. The identification and nomenclature of plant species is based on Rothmaler et al. (1990, 1991).

Bee communities

We made six transect records at regular intervals, each covering 30 min, on each field between April and August 1993 to measure species richness and abundance of wild bee communities. Along the transect, all bee species and flowering plant species visited by bees were recorded. If necessary, bees were caught for identification with a sweep net (\varnothing 40 cm). In addition, 100 sweeps through the vegetation at the height of the flower canopy and in the center of each field were

carried out at each transect during walking to sample small and inconspicuous species. Transect records were only done in sunny weather between 10 am and 5 pm. The time of day at which observations were made on a certain field was randomized on consecutive transect records.

Bee species were identified using Schmiedeknecht (1930). Additionally, we used Ebmer (1969–1971) for the genera *Lasioglossum* and *Halictus*, Dathe (1980) for the genus *Hylaeus*, Dorn and Weber (1988) for the genus *Megachile*, Warncke (1992) for the genus *Sphecodes*, Scheuchl (1996) for the genus *Coelioxys* and Mauss (1986) for the genera *Bombus* and *Psithyrus*. Nomenclature is based on Westrich (1989).

Life history traits

To assess successional changes of life history traits we calculated the weighted mean of body size and generation number per field using the following formula:

$$\bar{L} = \frac{\sum_{i=1}^S (N_i \times L_i)}{\sum_{i=1}^S N_i}$$

where \bar{L} represents the mean value of the life history trait, N_i the total number of observations of species i (summation is performed over all S species) and L_i the life history trait of species i (Steffan-Dewenter and Tschardt 1997). For other life history or community traits we calculated the proportion of individuals that were parasitic, social, oligolectic (using only one plant family or genus as pollen source) or soil-nesting. Ecological information was taken from Westrich (1989) and morphological data from the taxonomic literature mentioned above.

Statistical analysis

The statistical analyses of the data were performed using the software “Statgraphics plus for Windows 2.1”

Table 1. Field types studied.

Field type	Abbreviation	Number of replications	Successional stage
1-yr old set-aside fields sown with <i>Phacelia tanacetifolia</i>	Ph	4	–
1-yr old set-aside fields with naturally developed vegetation	S1	4	Pioneer
2-yr old set-aside fields with naturally developed vegetation	S2	4	
3-yr old set-aside fields with naturally developed vegetation	S3	4	Early
4-yr old set-aside fields with naturally developed vegetation	S4	4	
5-yr old set-aside fields with naturally developed vegetation	S5	4	
Orchard meadows (> 30 yr old)	Me	4	Mid

(Anon. 1995). If necessary, logarithmic or square root transformed variables were used to achieve normal distribution. Arcsine transformation ($\arcsin\sqrt{p}$ where p is a proportion) was used to achieve normal distribution for percentages (Sokal and Rohlf 1995). Stepwise multiple linear regression analyses were carried out to examine the possible joint effects of independent variables. Analyses of variance were used to test for differences between two or more groups, and group differences were established using the Tukey test at the 95 percent level. Spearman rank correlations (r_s) were used for the analysis of successional trends because data of field age were not normally distributed (Sokal and Rohlf 1995). In this case, *Phacelia* fields were excluded from the analysis because we did not consider them as a part of the successional gradient. The proportion of observed and expected flower visits on annual, biennial and perennial plants was compared by analysis of contingency tables (χ^2 -test). Arithmetic means \pm 1 SD are given in the text.

Results

Vegetation and resource availability

Altogether, we mapped 182 plant species on the plots established in the centre of each field. Species richness was significantly higher on the set-aside fields and orchard meadows than on the sown *Phacelia* fields ($F_{6,21} = 4.42$, $p = 0.005$). Species richness did not increase with successional age ($r_s = 0.088$, $n = 24$, $p = 0.67$). When we separated plant species into annuals (including winter annuals and biennials) and perennials, the mean number of annual plant species significantly declined from 24 ± 6 species in the first two years of succession to 12 ± 6 species in the fifth year up to $< 3 \pm 1$ species on the mid-successional meadows, whereas the mean number of perennial species increased from 8 ± 2 species in the first and 11 ± 4 in the second year of set-aside up to 39 ± 7 species on the meadows. Similarly, the proportion of annuals decreased from $83 \pm 10\%$ in the first to $28 \pm 25\%$ in the fifth year up to $3 \pm 1\%$ on the meadows. Cover of vegetation steadily increased with successional age from 64% on the one-year-old set-aside fields up to 97% on the mid successional meadows ($r_s = 0.817$, $n = 24$, $p < 0.001$). Resource availability of nectar and pollen was measured as both mean number and mean flower cover of actually flowering melittophilous plant species per field. Number of flowering plant species was lowest on *Phacelia* fields and highest on two-year-old set-aside fields and old meadows (Fig. 1A) and slightly increased with successional age ($r_s = 0.489$, $n = 24$, $p = 0.019$). The number of all plant species and the number of flowering melittophilous plant species were closely correlated in a simple regression analysis ($r^2 = 0.59$, $n = 28$,

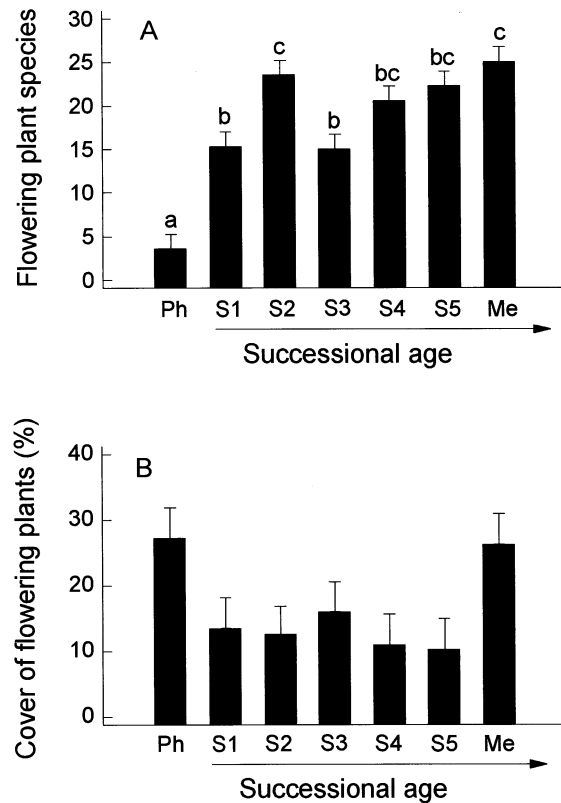


Fig. 1. Availability of nectar- and pollen-producing melittophilous plants on seven field types. Arithmetic means and pooled standard deviations are given. Significant differences are shown by different letters. Abbreviations: see Table 1. A) Mean number of flowering plant species: $F_{6,21} = 18.91$, $p < 0.001$. B) Mean cover of flowering plants: $F_{6,21} = 2.36$, $p = 0.067$.

$p < 0.001$). The mean percent cover of flowering plants was lower on the one- to five-year-old set-aside fields with naturally developed vegetation than on *Phacelia* fields and the orchard meadows (Fig. 1B, $r_s = 0.221$, $n = 24$, $p = 0.289$). However, the differences were only statistically significant if we pooled all naturally developed set-aside fields within one group ($F_{2,25} = 7.52$, $p = 0.003$). The number and percent cover of flowering plant species were not correlated ($r^2 = 0.076$, $n = 28$, $p = 0.66$).

Species richness and abundance of bees

Altogether, we recorded 2317 individuals of 129 wild bee species (Hymenoptera: Apoidea) in 21 genera. These are 29% of all bee species known from the German state Baden-Württemberg (Westrich 1989). Highest species richness was found in the genera *Andrena* and *Lasioglossum*, each with 28 species, the parasitic genera *Nomada* (16 species) and *Sphecodes* (12 species), and the genus *Halictus* (8 species). Along the

successional gradient, species richness of bees increased with age ($r_s = 0.431$, $n = 24$, $p = 0.039$). Species richness was highest on the mid successional meadows with 32 species, but unexpectedly high on the two-year-old set-aside fields with 29 species on average. The most species-poor bee communities were found on *Phacelia* fields with 13 and on one-year-old set-aside fields with

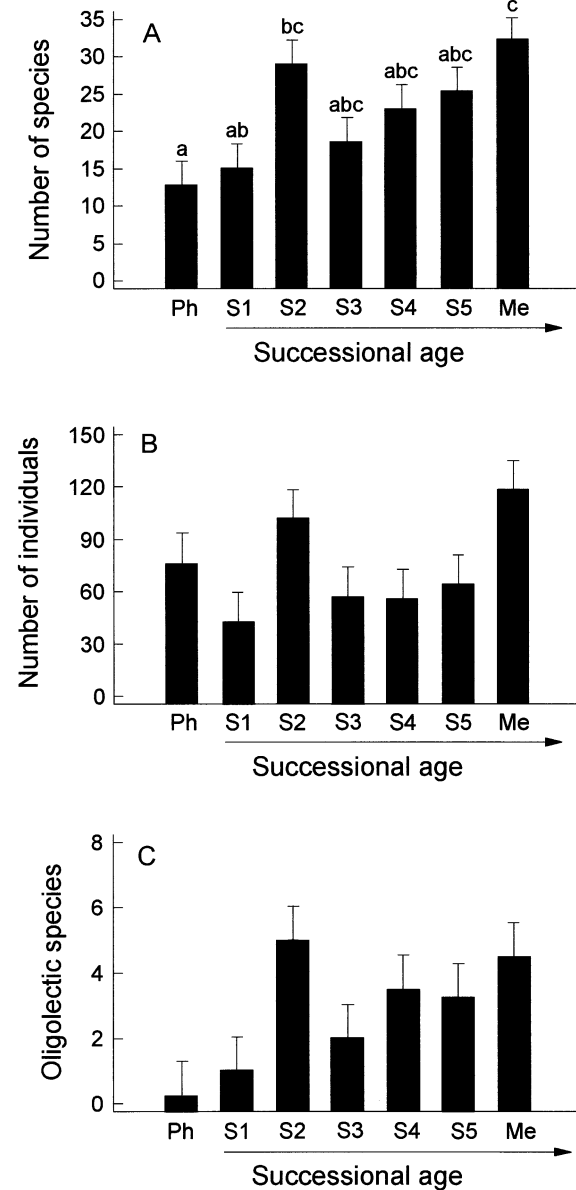


Fig. 2. Bee communities on one-year-old set-aside fields sown with *Phacelia*, one- to five-year-old set-aside fields with naturally developed vegetation and old orchard meadows. Arithmetic means and pooled standard deviations are given. Significant differences are shown by different letters. Abbreviations: see Table 1. A) Number of bee species per field: $F_{6,21} = 4.77$, $p = 0.003$. B) Number of bee individuals per field: $F_{6,21} = 2.39$, $p = 0.065$. C) Number of oligolectic bee species: $F_{6,21} = 2.88$, $p = 0.033$.

15 species on average (Fig. 2A). The abundance of wild bees was highest on meadows, two-year-old set-aside fields and *Phacelia*-fields, but differences between the seven field types were not significant (Fig. 2B). Furthermore, abundance of bees did not increase with successional age ($r_s = 0.231$, $n = 24$, $p = 0.268$). Abundance and species richness of wild bees were significantly correlated ($r^2 = 0.41$, $n = 28$, $p < 0.001$). We found 43 bee species that are endangered according to the red data list of Baden-Württemberg (Westrich 1989). The highest number of endangered bee species occurred on two-year-old set-aside fields and old meadows and the lowest on sown *Phacelia*-fields ($F_{6,21} = 3.40$, $p = 0.017$). The number of endangered bee species did not increase with successional age ($r_s = 0.158$, $n = 24$, $p = 0.448$).

Resource use of bee communities

Altogether we recorded 27 oligolectic bee species specialised in pollen collection for nest provisions on Asteraceae (9 species), Fabaceae (7), Brassicaceae (3), Campanulaceae (3), Ranunculaceae (1), Resedaceae (1), Dipsacaceae (1), Salicaceae (1) and Apiaceae (1). The number of oligolectic bee species was highest on two-year-old set-aside fields, but no significant successional trends existed (Fig. 2C, $r_s = 0.389$, $n = 24$, $p = 0.062$). On naturally developed set-aside fields we found some remarkable rare bee species like *Andrena distinguenda*, *Andrena lagopus* and *Andrena niveata* specialised on Brassicaceae. As expected, *Phacelia*-fields were unsuitable as food resources for specialised bee species (Fig. 2C) and were dominated by unspecialised, mainly social bee species of the genera *Lasioglossum* and *Bombus*, and by *Apis mellifera* (Table 2).

Effects of resource availability on species richness and abundance

Availability of nectar and pollen resources was measured in two ways: as species richness of flowering melittophilous plants and as percent flower cover of actually flowering plants. With stepwise multiple regression analyses we evaluated the relevance of resource availability and three independent habitat parameters (field size, total cover of vegetation, and habitat connectivity) for the distribution of bee diversity. The mean number of bee species per field increased with the species richness of flowering plants (Fig. 3A). In a multiple model a further 15.9% of the variance was explained by the cover of flowering plants ($Y = -0.07 + 0.94 \text{ richness} + 0.34 \text{ cover}$; $r^2 = 0.73$, $n = 28$, $p < 0.001$). The abundance of wild bees was mainly determined by the cover of flowering plants (Fig. 3B). In a multiple model we could explain further 12.2% of the variance by the number of species of flowering

Table 2. Life history traits and community structure of bees on one-year-old set-aside fields with *Phacelia*, one- to five-year-old set-aside fields with naturally developed vegetation and old orchard meadows. Arithmetic means and individual standard deviations, F- and p-values of one-way Anova (n = 28) and r_s and p-values of Spearman rank correlation (n = 24, excluding *Phacelia*-fields) are given for each factor. Significant differences are shown by different letters. Abbreviations see Table 1.

Factor	Ph	S1	S2	S3	S4	S5	Me	F _{6,21}	P	r_s	P _s
Body size (mm)	8.54 ± 0.2 ^b	7.44 ± 0.5 ^{ab}	6.65 ± 0.43 ^a	7.32 ± 0.22 ^{ab}	7.60 ± 0.17 ^{ab}	7.19 ± 0.33 ^{ab}	6.75 ± 0.64 ^{ab}	2.36	0.067	-0.41	0.035
Generations yr ⁻¹	1.19 ± 0.07	1.31 ± 0.10	1.18 ± 0.06	1.33 ± 0.10	1.23 ± 0.03	1.23 ± 0.04	1.08 ± 0.02	1.78	0.152	-0.25	0.196
Eusocial bees (%)	70.45 ± 5.82 ^b	40.05 ± 9.26 ^a	53.03 ± 6.10 ^{ab}	45.64 ± 2.74 ^{ab}	46.33 ± 4.36 ^{ab}	43.60 ± 6.27 ^a	61.81 ± 1.77 ^{ab}	3.73	0.011	-0.145	0.462
Parasitic bees (%)	6.64 ± 2.69 ^a	11.20 ± 3.78 ^{ab}	17.99 ± 4.72 ^{ab}	16.70 ± 6.36 ^{ab}	23.31 ± 3.55 ^b	16.36 ± 2.03 ^{ab}	12.10 ± 1.69 ^{ab}	2.38	0.065	0.294	0.126
Oligolectic bees (%)	0.60 ± 0.6	8.87 ± 4.76	8.58 ± 3.19	4.09 ± 1.53	8.19 ± 2.69	8.09 ± 2.73	6.74 ± 1.81	1.22	0.33	0.011	0.960
Soil-nesting bees (%)	95.82 ± 2.57	100 ± 0.0	91.17 ± 3.70	94.98 ± 2.90	89.02 ± 1.70	90.68 ± 6.32	88.71 ± 2.71	1.53	0.216	-0.414	0.047

plants ($Y = 0.40 + 2.26 \text{ cover} + 1.97 \text{ richness}$; $r^2 = 0.45$, $n = 28$, $p < 0.001$). The other habitat parameters did not significantly contribute to the models.

Species diversity of flower-visiting bees

During transect records we observed 896 flower-visits of 104 bee species on 82 plant species. These flower-visitor communities showed great differences in species richness and abundance of flower-visiting bees. The plant species with the most species-rich bee communities were the perennial weeds *Daucus carota*, *Taraxacum officinale*, *Picris hieracioides*, *Ranunculus repens* and *Cirsium arvense* with 15–28 bee species and the annuals *Sinapis arvensis*, *Matricaria maritima*, *Myosotis arvensis*, *Medicago lupulina*, *Senecio vernalis* and *Crepis capillaris* with 8–26 bee species. The biennials with the

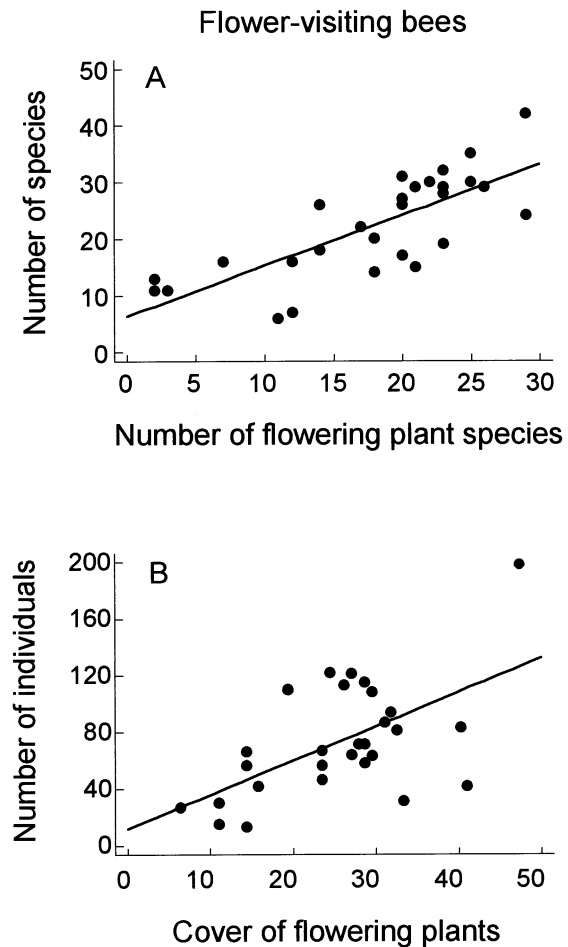


Fig. 3. Effects of resource availability on species richness and abundance of bees. A) Relation between the number of bee species and the mean number of flowering plant species per field: $Y = 6.36 + 0.89X$, $F = 34.89$, $n = 28$, $r^2 = 0.573$, $p < 0.001$. B) Relation between the number of bee individuals and the mean cover of flowering plants per field: $Y = 11.94 + 2.41X$, $F = 12.96$, $n = 28$, $r^2 = 0.333$, $p = 0.001$.

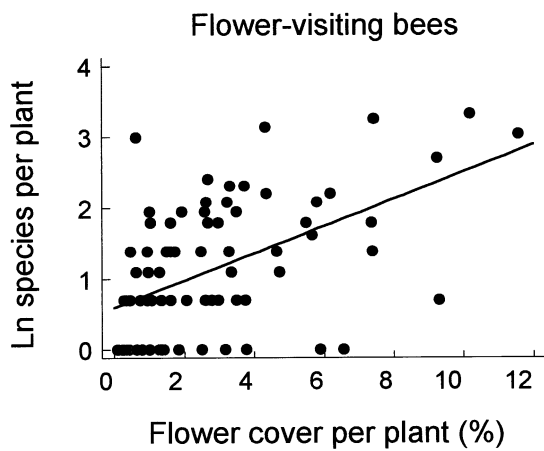


Fig. 4. Relationship between species richness of flower-visiting bees per plant and mean cover of flowers per plant: $\text{Ln}Y = 0.59 + 0.19 \arcsin\sqrt{X}$, $F = 30.45$, $n = 82$ (plant species), $r^2 = 0.281$, $p < 0.001$.

most species-rich flower-visitors were *Reseda lutea* and *Erigeron annuus* with 7 and 9 flower-visiting bee species, respectively. The number of flower-visiting bee species per plant was positively correlated with the mean percent cover of flowers per plant species (Fig. 4) whereas the life form, i.e. whether they were annuals, biennials or perennials, did not explain differences in species richness ($F = 0.27$, $n = 82$, $p = 0.76$). We obtained a very similar result when we included the cover of flowers as cofactor ($F = 0.08$, $n = 82$, $p = 0.92$).

Hypotheses suggest that annual plants are less attractive for large social bees than perennial plants. Therefore, we analysed the flower-visitation rates of bees on annual and perennial plants in more detail. With increasing successional age the number of observed flower visits on annual plants declined ($r_s = -0.421$, $n = 20$, $p = 0.066$) whereas the number of flower visits on perennial plants increased ($r_s = 0.528$, $n = 20$, $p = 0.022$). This could be expected because of the changing cover of annual and perennial plants during succession. Therefore, we compared the observed proportion of flower-visiting bees on annual, biennial and perennial flowers with the expected distribution of flower-visitors due to the proportion of annuals, biennials and perennials of the total cover of flowering plants. We found that annual and biennial flowers were visited more frequently than expected, whereas flower-visits on perennial plants were under-represented (Fig. 5A). Furthermore, we compared the deviation of the proportion of flower-visiting bees of five families from the mean proportion of all observed individuals on annuals, biennials and perennials. The families Megachilidae, Apidae and Anthophoridae significantly preferred perennials, whereas the Halictidae and Andrenidae showed a slight tendency to prefer annuals, but it was not significant (Fig. 5B).

Successional patterns of life history traits

Life history traits are assumed to vary during succession. Here, we tested body size, number of generations, proportion of parasitic bees, proportion of social bees, food specialisation, and nesting behaviour. Mean body size and proportion of parasitic bees did not significantly change during succession (Table 2). Only flower-visiting bees on *Phacelia* fields were larger than on successional stages with naturally developed vegetation and the proportion of parasitic bees was lower on *Phacelia* fields than on four-year-old set-aside fields (Table 2). The mean number of generations differed significantly between mid-successional meadows (1.08 ± 0.14) and pioneer and early-successional stages (1.26 ± 0.14) only when we pooled all naturally developed set-aside fields into one group ($F_{2,25} = 3.42$, $p = 0.049$). The proportion of social bees (except *Apis*) was highest on sown fields and mid-successional meadows (Table 2). Abundance of flower-visiting honey bees was significantly higher on *Phacelia* fields than on all remaining field types ($F_{6,21} = 8.93$, $p < 0.001$). Bee communities of mid-successional stages did not show a higher degree of food specialisation than those of pioneer or early-successional stages (Table 2). The proportion of soil-nesting bees decreased with successional age

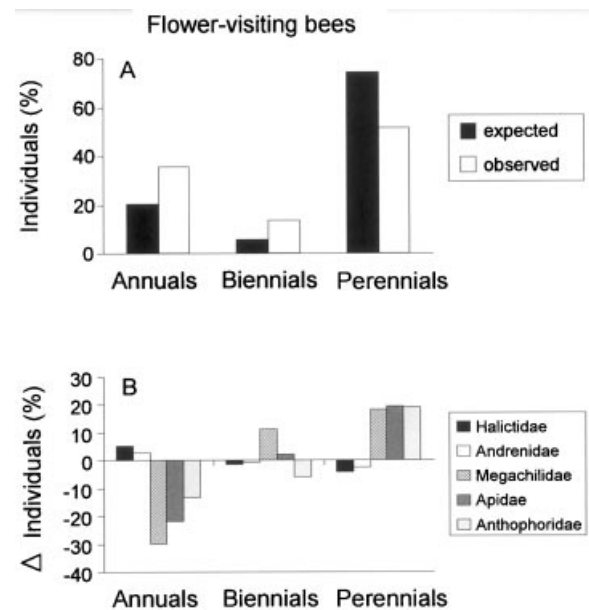


Fig. 5. Flower-visiting bees on annual, biennial and perennial plant species. A) Comparison of observed and expected proportions of individuals based on 896 observations of flower visits of 104 bee species on 82 plant species. $\chi^2 = 11.38$, $p = 0.003$. B) Deviation of the proportion of individuals of five bee families from the mean proportion of all observed individuals on annuals, biennials and perennials. Halictidae: $\chi^2 = 0.55$, $p = 0.761$, Andrenidae: $\chi^2 = 0.20$, $p = 0.904$, Megachilidae: $\chi^2 = 29.42$, $p < 0.001$, Apidae (excluding *Apis mellifera*): $\chi^2 = 12.92$, $p = 0.002$, Anthophoridae: $\chi^2 = 10.08$, $p = 0.007$.

(Table 2) whereas the proportion of above-ground nesting bees significantly increased ($r_s = 0.413$, $n = 24$, $p = 0.048$).

Discussion

In this study we analysed bee communities along a successional gradient focusing on 1) patterns of species richness and abundance, 2) effects of plant succession on resource availability and resource use and 3) changes of life history. Furthermore we were interested in the effects of management (sown or naturally vegetated set-aside fields), and age for the conservation value of these habitats for bees. We divided secondary succession into pioneer successional stages (the first two years), dominated by annuals, early successional stages (from the third year onwards) where perennials establish, and mid successional stages (> 30 yr old orchard meadows).

Patterns of species diversity along a successional gradient

Successional theory predicts increasing species richness with successional age (Odum 1969, Brown and Southwood 1987), but patterns differ with respect to the studied insect group (e.g. Brown and Southwood 1983, Brown and Hyman 1986, Greiler 1994). Our results showed that secondary succession is not as linear as expected. Species richness of bees was highest on two-year-old set-aside fields and mid-successional orchard meadows, so a bimodal curve resulted. Interestingly, butterflies showed similar patterns of species richness in that two-year-old set-aside fields harboured more species than other types of set-aside, although the two-year-old set-aside fields in the butterfly study and this bee study were not identical (Steffan-Dewenter and Tscharnkte 1997). Therefore, it is very probable that the peak diversity of two-year-old set-aside fields was not a result by chance but a more general successional pattern of these species groups. Successional patterns of bee communities may depend on 1) colonisation ability, 2) habitat quality which should be mainly determined by successional changes of vegetation and 3) biotic interactions like competition or predation. The high species richness on two-year-old set-aside fields showed that bees were better colonisers than expected from their well-known nest-site fidelity (Westrich 1989, Potts and Willmer 1997). Successional changes of vegetation should be a major determinant of habitat quality for insects (Brown and Southwood 1987), but in contrast to expectations plant species richness did not continuously increase with habitat age. The most striking pattern was the rapid change from annual vegetation in the first two years of succession to perennial vegetation

from the third year onwards. We found that in the second year of succession, where annuals were still and perennials already present, species richness of flowering plants was as high as on the orchard meadows. Species richness of flowering plants was the best predictor of species richness of bees, whereas the cover of flowering plants best predicted bee abundance. Thus, our results confirm the general expectation that more diverse vegetation supports more diverse insect communities (Strong et al. 1984, Siemann et al. 1998), also shown for butterflies (Steffan-Dewenter and Tscharnkte 1997) and trap-nesting bees (Gathmann et al. 1994). The non-linear change of plant species richness during succession was therefore paralleled by a peak of bee diversity in the second year of succession.

Resource use

The resource use of bee communities was studied in more detail with respect to 1) the distribution of specialised bee species, 2) the value of plant species as nectar or pollen sources and 3) the preference for annual, biennial or perennial plant species. Generally, pioneer and early successional fields are expected to be dominated by short-lived, unspecialised and common species (Brown and Southwood 1987, Corbet 1995). In our study, we recorded rare bee species specialised on annual weeds like *Sinapis arvensis* on two-year-old set-aside fields, underlining the peculiarity of pioneer successional stages. Such a preference for pioneer and early successional stages by specialised species was also found for the butterflies *Issoria lathonia* feeding on the annual *Viola arvensis* (Steffan-Dewenter and Tscharnkte 1997), *Mellicta athalia* feeding on *Melampyrum pratense* (Thomas et al. 1992) and the weevil *Ceuthorhynchus erysimi* (Curculionidae) feeding on *Capsella bursa-pastoris* (Greiler 1994).

High abundance and species richness of flower-visiting bees was observed on *Cirsium arvense*, *Taraxacum officinale*, *Ranunculus repens* and *Crepis capillaris*, underlining the importance of weeds as nectar and pollen sources. Common hypotheses suggest that annual plants are less nectar-rich and less apparent for bees and therefore are less attractive for large and long-tongued bees of the families Megachilidae and Apidae (Parrish and Bazzaz 1979, Corbet 1995). We could confirm this expectation and further showed that Anthophoridae significantly preferred perennials, whereas Halictidae and Andrenidae tended to prefer annuals, but this was not significant. Interestingly, the general pattern was different from the expectation that annuals are not important as nectar and pollen sources for bees. We found that annual, biennial and perennial plant species were visited by similar numbers of bee species and that annuals and biennials were visited more often

than expected from their abundance, whereas perennials were visited less often than expected. Possibly, the bee communities of pioneer or early-successional fields are adapted to the vegetation typical for these successional stages and therefore preferred annual plants to some extent.

Life history traits

Variation in life history traits across successional gradients are of special interest to determine mechanisms of succession (Grime 1977, Brown and Southwood 1987, Huston and Smith 1987, Tilman 1990). Results of Steffan-Dewenter and Tscharntke (1997) showed decreasing body size, migrational ability and generation time with increasing successional age for butterflies. Similar patterns were found for Heteroptera (Brown 1985). However, the ecological traits of bees in our study showed only weak successional tendencies. Mean body size did not vary between pioneer, early and mid-successional stages, but differed only between sown and naturally developed set-aside fields. This may have the following reasons: 1) migrational ability was not correlated with body size, i.e. both small and large bees had the same chance to colonise the new habitats (but see Gathmann et al. 1994), 2) differences in migrational ability were less important because habitat isolation did not restrict colonisation, and 3) advantages of larger bees with respect to higher migrational ability were compensated for by the better adaptation of smaller bees to the less nectar-rich annual flowers of pioneer-successional stages (Parrish and Bazzaz 1979, Corbet 1995). Number of generations was higher in pioneer- and early- than in mid-successional stages. This supports the hypotheses that in unpredictable habitats, rapid reproduction is of selective advantage, as previously shown for Heteroptera (Brown 1985), Auchenorrhyncha (Novotny 1994) and Lepidoptera (Hodgson 1993, Steffan-Dewenter and Tscharntke 1997). The preference for mid-successional habitats by social bees may be due to their dependence on a diverse and high-value nectar and pollen supply during the whole season (Fussell and Corbet 1992). The proportions of parasitic bees were similar in pioneer, early and mid successional stages. Therefore, our data do not support the expectation that biotic interactions like parasitism and predation increase with successional age (Southwood 1988). Increasing degree of food specialisation during succession has been expected due to higher species packing and smaller niche breadth (Brown and Southwood 1983), but in our study, the proportion of oligolectic species was similar in all successional stages. One reason is obviously that bees oligolectic on annuals can only be present in the early years. The cover of vegetation increased during succession and this was presumably paralleled by a

decrease in the availability of open and sunny patches of soil, favoured by many ground-nesting species (Potts and Willmer 1997). In correspondence with this change in vegetation, the proportion of ground-nesting bees decreased with successional age, whereas that of above-ground nesting bees increased. In conclusion, we could not find clear differences in life history traits during succession. Successional patterns of bee communities appeared to depend on the successional variation of available food plants and nesting sites, but presumably not on the competitive exclusion of certain species due to competitors with adaptations to a particular successional stage.

Nature conservation and set-aside

Since 1988, set-aside has occurred in the European community on up to 15% of the cropped area and therefore has a high potential influence on the diversity of agricultural landscapes. Although set-aside was used primarily to reduce overproduction, it may also open new possibilities for nature conservation (Corbet 1995). This is of special importance because large areas of arable land in Europe are unfavourable for bees and other insects, resulting in loss of species diversity and ecological functions like pollination (e.g. Osborne et al. 1991, Banaszak 1992, Allen-Wardell et al. 1998, Steffan-Dewenter and Tscharntke 1999). Pioneer and early successional set-aside fields are often expected to have a low conservation value, mainly supporting common weeds and pest insects. This may be true in structurally simple and intensively used agricultural landscapes, but not in structurally more complex and more extensively used agricultural landscapes. In our study in a complex landscape, we found species-rich bee communities with many specialised and endangered species on these little acknowledged set-aside fields, as long as they had naturally developed vegetation. In contrast, set-aside fields sown with *Phacelia tanacetifolia* supported only little diverse bee communities consisting of unspecialised, common, mainly social bees. Such sown fields did not provide suitable nesting sites, so they were only partial habitats. Similar results were found for butterflies (Steffan-Dewenter and Tscharntke 1997). Therefore, natural regeneration or species-rich seed mixtures should be preferred instead of sowing *Phacelia*. Generally, we agree with Corbet (1995) that semi-natural and old habitats are most important for nature conservation in the agricultural landscape. However, our results suggest that one- to five-year-old set-aside fields with naturally developed vegetation will significantly add to habitat diversity in the agricultural landscape and enhance plant and insect populations specialised on pioneer and early successional habitats.

Acknowledgements – We greatly thank S. A. Corbet, R. Dolch and C. O'Toole for useful comments and suggestions, H.-J. Greiler and S. Marci for advice, field assistance and discussions, M. Schwarz, H. Riemann, K. Schmidt and P. Westrich for help in species identification, and the German Science Foundation for financial support.

References

- Allen-Wardell, G. et al. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop fields. – *Conserv. Biol.* 12: 1–11.
- Anon. 1995. *Statgraphics plus for Windows*, ver. 2.1. – Manugistics, Rockville, Maryland.
- Banaszak, J. 1992. Strategy for conservation of wild bees in an agricultural landscape. – *Agricult. Ecosyst. Environ.* 40: 179–192.
- Bauer, M. and Engels, W. 1991. Bienenweide auf stillgelegten Ackerflächen. – *Allgemeine Deutsche Imkerzeitung* 4: 40–43.
- Bazzaz, F. A. 1975. Plant species diversity in old-field successional ecosystems in southern Illinois. – *Ecology* 56: 485–488.
- Bazzaz, F. A. 1996. *Plants in changing environments*. – Cambridge Univ. Press.
- Brown, V. K. 1985. Insect herbivores and plant succession. – *Oikos* 44: 17–22.
- Brown, V. K. and Southwood, T. R. E. 1983. Trophic diversity, niche breadth and generation times of exopterygote insects in a secondary succession. – *Oecologia* 56: 220–225.
- Brown, V. K. and Hyman, P. S. 1986. Successional communities of plants and phytophagous Coleoptera. – *J. Ecol.* 74: 963–975.
- Brown, V. K. and Southwood, T. R. E. 1987. Secondary succession: patterns and strategies. – In: Gray, A. J., Crawley, M. J. and Edwards, D. J. (eds), *Colonization, succession and stability*. – Blackwell, pp. 315–337.
- Connell, J. H. and Slatyer, R. O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. – *Am. Nat.* 111: 1119–1144.
- Corbet, S. A. 1995. Insects, plants and succession: advantages of long-term set-aside. – *Agricult. Ecosyst. Environ.* 53: 201–217.
- Corbet, S. A., Williams, I. H. and Osborne, J. L. 1991. Bees and the pollination of crops and wild flowers in the European community. – *Bee World* 72: 47–59.
- Corbet, S. A. et al. 1995. The competition box: a graphical aid to forecasting pollinator performance. – *J. Appl. Ecol.* 32: 707–719.
- Dathe, H. H. 1980. Die Arten der Gattung *Hylaeus* F. in Europa (Hymenoptera: Apoidea, Colletidae). – *Mitt. des Zool. Mus. Berlin* 56: 207–294.
- Dorn, M. and Weber, D. 1988. Die Luzerne-Blattschneiderbiene und ihre Verwandten in Mitteleuropa. – Neue Brehm-Bücherei, Wittenberg.
- Ebmer, A. W. 1969–1971. Die Bienen des Genus *Halictus* Latr. S. L. im Großraum von Linz (Hymenoptera, Apidae). Systematik, Biogeographie, Ökologie und Biologie mit Berücksichtigung aller bisher aus Mitteleuropa bekanntgewordenen Arten. – *Naturkundliches Jahrbuch der Stadt Linz* 1969: 133–183, 1970: 19–82, 1971: 63–156.
- Edward-Jones, G. and Brown, V. K. 1993. Successional trends in insect herbivore population densities: a field test of a hypothesis. – *Oikos* 66: 463–471.
- Fussell, M. and Corbet, S. A. 1992. Flower usage by bumblebees: a basis for forage plant management. – *J. Appl. Ecol.* 29: 451–465.
- Gathmann, A., Greiler, H.-J. and Tscharnkte, T. 1994. Trap-nesting bees and wasps colonizing set-aside fields: succession and body size, management by cutting and sowing. – *Oecologia* 98: 8–14.
- Greiler, H.-J. 1994. *Insektengesellschaften auf selbstbegrüntem und eingesäten Ackerbrachen*. – Paul Haupt, Bern.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. – *Am. Nat.* 111: 1169–1194.
- Hodgson, J. G. 1993. Commonness and rarity in British butterflies. – *J. Appl. Ecol.* 30: 407–427.
- Hölzinger, J. 1981. *Die Vögel Baden-Württembergs*, Band 4. – LfU Baden-Württemberg, Karlsruhe.
- Huston, M. and Smith, T. 1987. Plant succession: life history and competition. – *Am. Nat.* 130: 168–198.
- Mauss, V. 1986. *Bestimmungsschlüssel für Hummeln*. – Deutscher Jugendbund für Naturbeobachtung, Hamburg.
- Neff, J. L. and Simpson, B. B. 1993. Bees, pollination systems and plant diversity. – In: LaSalle, J. and Gauld, I. D. (eds), *Hymenoptera and biodiversity*. CAB International, Wallingford, pp. 143–168.
- Novotny, V. 1994. Life histories of leafhoppers (Auchenorrhyncha) in permanent and ephemeral habitats. – *Behav. Ecol. Sociobiol.* 25: 93–95.
- Odum, E. P. 1969. The strategy of ecosystem development. – *Science* 164: 262–270.
- Osborne, J. L., Williams, I. H. and Corbet, S. A. 1991. Bees, pollination and habitat change in the European Community. – *Bee World* 72: 99–116.
- O'Toole, C. 1993. Diversity of native bees and agroecosystems. – In: LaSalle, J. and Gauld, I. D. (eds), *Hymenoptera and biodiversity*. CAB International, Wallingford, pp. 169–196.
- Parrish, J. A. and Bazzaz, F. A. 1979. Differences in pollination niche relationships in early and late successional plant communities. – *Ecology* 60: 597–610.
- Potts, S. G. and Willmer, P. 1997. Abiotic and biotic factors influencing nest-site selection by *Halictus rubicundus*, a ground-nesting halictine bee. – *Ecol. Entomol.* 22: 319–328.
- Rothmaler, W. et al. 1990. *Exkursionsflora Gefäßpflanzen*, Band 2. – Volk und Wissen Verlag, Berlin.
- Rothmaler, W. et al. 1991. *Exkursionsflora Atlas der Gefäßpflanzen*, Band 3. – Verlag Volk und Wissen, Berlin.
- Scheuchl, E. 1996. *Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs*, Band II: Megachilidae–Melittidae. – Eigenverlag, Velden.
- Schmiedeknecht, O. 1930. *Die Hymenopteren Nord- und Mitteleuropas*. – Gustav Fischer, Jena.
- Schottmüller, H. 1961. Der Löß als gestaltender Faktor in der Kulturlandschaft des Kraichgaus. – *Forschungen zur Deutschen Landeskunde* 130: 1–96.
- Siemann, E. et al. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. – *Am. Nat.* 152: 738–750.
- Siemann, E., Haarstad, J. and Tilman, D. 1999. Dynamics of plant and arthropod diversity during old field succession. – *Ecography* 22: 406–414.
- Sokal, R. R. and Rohlf, F. 1995. *Biometry*. – Freeman.
- Southwood, T. R. E. 1988. Tactics, strategies and templets. – *Oikos* 52: 3–18.
- Stedmann, B. 1994. Government and European Union land use policy. – In: Matheson, A. (ed.), *Forage for bees in an agricultural landscape*. Int. Bee Res. Assoc., Cardiff, pp. 3–6.
- Steffan-Dewenter, I. and Tscharnkte, T. 1997. Early succession of butterfly and plant communities on set-aside fields. – *Oecologia* 109: 294–302.
- Steffan-Dewenter, I. and Tscharnkte, T. 1999. Effects of habitat isolation on pollinator communities and seed set. – *Oecologia* 121: 432–440.
- Strong, D. R., Lawton, J. H. and Southwood, R. 1984. *Insects on plants*. – Blackwell.
- Thomas, C. D., Thomas, J. A. and Warren, M. S. 1992. Distribution of occupied and vacant butterfly habitats in fragmented landscapes. – *Oecologia* 92: 563–567.
- Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. – *Oikos* 58: 3–15.

- Tramer, E. J. 1975. The regulation of plant species diversity on an early successional old-field. – *Ecology* 56: 905–914.
- Tscharntke, T. et al. 1996. Die Flächenstillegung in der Landwirtschaft-eine Chance für Flora und Fauna der Agrarlandschaft? – *NNA-Berichte (Alfred-Töpfer-Akademie für Naturschutz Schneverdingen)* 9: 59–72.
- Warncke, K. 1992. Die westpaläarktischen Arten der Biengattung *Sphecodes* Latr. (Hymenoptera, Apidae, Halictinae). – *Berichte der Naturforschenden Gesellschaft Augsburg* 52: 9–64.
- Westrich, P. 1989. *Die Wildbienen Baden-Württembergs*. – Eugen Ulmer, Stuttgart.
- Williams, I. H. 1996. Aspects of bee diversity and crop pollination in the European Union. – In: Matheson, A. et al. (eds), *The conservation of bees*. Academic Press, pp. 63–80.
- Williams, I. H. and Carreck, N. L. 1994. Land use changes and honey bee forage plants. – In: Matheson, A. (ed.), *Forage for bees in an agricultural landscape*. Int. Bee Res. Assoc., Cardiff, pp. 7–20.