Differential responses of bumblebees and diurnal Lepidoptera to vegetation succession in long-term set-aside

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Summary

1. Establishing temporal habitat patches, such as long-term set-aside, is potentially a valuable approach to support pollinator populations in intensively cultivated landscapes. The benefits of this approach are expected to differ between pollinator groups, because of fundamental differences in their ecology.

2. We studied the responses of two pollinator groups, bumblebees and diurnal Lepidoptera (butterflies and diurnal moths), to the vegetation succession in experimental set-aside during six consecutive years. The pollinators were monitored in 24 large treatment plots (50 × 50 m), sown with three different seed mixtures (competitive and two alternatives) and unmanaged or managed by mowing, and on 10 surrounding field margins.

3. The responses of the two pollinator groups to vegetation succession were distinctly different. Bumblebees showed a very strong positive response to the diverse seed mixture with abundant floral resources, and their abundance peaked in the first year. The species richness and abundance of Lepidoptera were increased gradually, suggesting differential colonization speeds of species and a gradual establishment of populations. Lepidopteran abundance reached the level of the field margins in 3 years, whereas the corresponding species richness level was not reached. The benefits of the alternative seed mixtures were less pronounced in Lepidoptera than in bumblebees. No effects of the mowing treatment on either species group were detected.

4. Within both pollinator groups, the response to vegetation succession was associated with species traits. In bumblebees, long-tongued species (indicating specialization) were increased during succession. In butterflies and diurnal moths, colonization success of species was strongly correlated with their wing span (indicating mobility). The most successful colonizers in butterflies were grass feeders and in diurnal moths the species feeding on leguminous plants at the larval stage.

5. *Synthesis and applications.* The ecological requirements of different pollinator groups should be taken into account when establishing set-aside. Supporting bumblebees is possible even on short-term set-aside, assuming nectar and pollen sources are made available. The occurrence of butterflies and diurnal moths is strongly driven by additional factors, such as the availability of larval host plants as well as adult mobility, which calls for set-aside management regimes to be in place for several years.

Key-words: biodiversity, colonization, fallow experiment, field margin, mowing, pollinator, seed mixture, set-aside duration, species traits, spring cereal

Introduction

In many parts of northern Europe, modern agricultural landscapes are dominated by cereal production on large field

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parcels (Stoate *et al.* 2001) with only a small proportion of semi-natural habitat, such as traditionally managed grassland and field margins (Ekroos, Heliölä & Kuussaari 2010; Persson *et al.* 2010). Set-aside fields are partly expected to compensate for the loss of these habitats (Corbet 1995; Critchley & Fowbert 2000) and can thus potentially help support farmland biodiversity as well as provide valuable ecosystem services, such as pollination (Isaacs *et al.* 2009). The patterns and mechanisms of secondary succession on arable land have been investigated extensively (Cramer & Hobbs 2007) but experimental studies remain scarce and have concentrated on the structure of plant (e.g. Harpole & Tilman 2006) rather than insect communities. More detailed understanding of community assembly in novel habitats calls for experimental evidence (Temperton *et al.* 2004). In the case of plant–insect interactions on set-aside, consideration of the ecological differences both between and within insect groups in the context of the establishment and management options for set-aside is required.

Bumblebees and diurnal Lepidoptera – two important pollinator groups occurring on set-aside – differ in their co-evolutionary relationships with plants. In bumblebees, adults feed on nectar whereas pollen is fed to the larvae inside the nest. Because of the effective communication between these social insects, workers rapidly exploit newly found flowering patches (Carvell *et al.* 2007). Lepidopteran species have an additional co-evolutionary history with their larval host plants. The occurrence of diurnal Lepidoptera is, therefore, strongly driven not only by the availability of nectar resources for adults but by the coverage of suitable host plants (Clausen, Holbeck & Reddersen 2001). This coverage is expected to gradually increase as vegetation succession proceeds, whereas flowers can be made available more rapidly by sowing suitable plants. In addition, the colonization speed of novel set-aside plots can be expected to vary within the pollinator groups, according to differences in niche breadth and dispersal capacity between species. These two species traits are known to play a crucial role in insect community organization (Williams *et al.* 2010).

In bumblebees, niche breadth can be defined by tongue length. Long-tongued bumblebees can be considered a more specialized group than short-tongued species (Öckinger & Smith 2007), because long-tongued species mainly forage on flowers with long corolla tubes. Short-tongued species also forage on such flowers by robbing the flowers (Kudo *et al.* 2004), and in addition, they forage on more open flower types. In diurnal Lepidoptera, niche breadth can be defined by larval specificity together with the larval host plant type. In terms of larval specificity, monophagous species feed on a single plant species and oligophagous species on one plant genus, whereas polyphagous species have a wider variety of host plants (Komonen *et al.* 2004). With regard to larval host plant type, species tend to feed on certain kinds of plants; for example, species feeding on woody plants are usually strongly associated with forests. Finally, adult mobility and thus the ability to colonize new habitat patches varies between species in butterflies and diurnal moths. In butterflies, mean forewing length (indicating mobility) has been found to decrease with set-aside age (Steffan-Dewenter & Tscharntke 1997).

Here, we experimentally studied the community assembly of bumblebees and diurnal Lepidoptera on set-aside. We contrasted a commonly used competitive mixture of grasses and clover (Tattersall *et al.* 2000) with two alternative mixtures providing more resources for pollinators (Pywell *et al.* 2002; Carvell *et al.* 2007). Mowing was carried out to make the vegetation more attractive to pollinators (Gathmann, Greiler & Tscharntke 1994) via changes in plant community structure and increased plant species richness (Hansson & Fogelfors 1998; Walker *et al.* 2004). Pollinators were monitored annually for 6 years to document their colonization and establishment processes and to understand the underlying mechanisms affecting them. Additional data were collected from surrounding field margins in an untreated control habitat to detect annual population fluctuations attributed to factors such as variable weather conditions (Roy *et al.* 2001). We expected to find differential responses of bumblebees and diurnal Lepidoptera to vegetation succession in set-aside, based on the fundamental differences in their ecology. In addition, we expected the responses of the pollinator groups to be associated with species traits.

Materials and methods

EXPERIMENTAL DESIGN AND STUDY AREA

We conducted a 6-year field experiment to examine the succession of pollinator communities on long-term set-aside. On the experimental set-aside plots, the effects of two factors (sown seed mixture and mowing) were studied. Furthermore, the pattern of succession was compared with the pattern seen on untreated field margins.

The experiment was conducted from 2003 to 2008 on a large clay soil field parcel as a strip plot design (Appendix S1, Supporting Information). The study plots were 0·25 ha (50 × 50 m) in size. The study area in Ypäjä, south-western Finland (ETRS-TM35FIN N 6745551 E 299807), was situated in a landscape dominated by spring cereal production, with scattered areas of coniferous forest. For comparison with the experimental study plots, we also monitored the pollinators on 10 surrounding, uncultivated field margins situated within 0–850 m from the study field.

At the outset, two mowing treatments were assigned randomly to each study plot (n = 24) by columns and three seed mixtures by rows. The seed mixture treatments were the competitive (standard) grass mixture, a less competitive grass mixture and a diverse nectar and pollen plant seed mixture. The competitive mixture included *Festuca pratensis* and *Phleum pratense*, and red clover *Trifolium pratense*. The less competitive mixture included *Agrostis capillaris* and *Festuca ovina*. In the diverse mixture, *A. capillaris* and *F. ovina* were sown together with 12 nectar and pollen plant species (Appendix S1, Supporting Information) chosen according to an expert evaluation. The habitat management treatment was either annual mowing (with a mower chopper between 28 August and 5 October) or no mowing.

POLLINATOR MONITORING

The monitoring was carried out using the standard line-transect method (Pollard & Yates 1993). On the set-aside, a 250-m-long transect passed through each study plot in a serpentine manner, and on the field margins, a 250-m-long sector of each field margin was monitored. In both habitats, a permanent route was walked at a steady

speed and all individuals within a 5×5 m square ahead were recorded. The counts were carried out four times each summer at approximately 2-week intervals in weather conditions allowing insect activity (for minimum weather requirements, see Pollard & Yates 1993), the first count being made in the first half of June and the last count at the end of July.

The bumblebees (nomenclature according to Söderman & Vikberg 2002), butterflies and diurnal moths (nomenclature according to Kullberg *et al.* 2002) were identified to species except cuckoo bumblebees (former genus *Psithyrus* in bumblebees) which were identified to genus level. The group of diurnal moths included all macrolepidopteran species other than butterflies, which were either actively in flight or were flushed from the vegetation during the counts. When an insect was observed visiting a flower, the plant species was also recorded (nomenclature according to Hämet-Ahti *et al.* 1998) to show which plant species were important nectar and pollen sources during each study year and for which pollinator group. In the case of the diverse mixture, this allowed us to formulate recommendations in terms of the optimal plant species composition.

VEGETATION SAMPLING

The vegetation of the set-aside plots was studied to monitor its succession during the 6-year experiment and to estimate its role in the succession of pollinator communities. The first sampling was conducted each year between 24 June and 4 July and the second between 22 July and 11 August.

All the plant species in each study plot ($n = 24$) were recorded, and the coverage of each species was estimated as a percentage of the area of the entire plot (50×50 m) with a nine-step scale: $1 = x < 0.125\%$, $2 = 0.125\% < x < 0.5\%$, $3 = 0.5\% < x < 2\%$, $4 = 2\% < x < 4\%$, $5 = 4\% < x < 8\%$, $6 = 8\% < x < 16\%$, $7 = 16\% < x < 32\%$, $8 = 32\% < x < 64\%$ and $9 = x > 64\%$. Using the same procedure, the species richness and coverage of insect-pollinated plants in flower at the time of sampling were recorded separately. Insect-pollinated species were listed based on the BiolFlor data base (Klotz, Kühn & Durka 2002).

The recorded plant species were further divided into grasses (Poaceae) and non-Poaceae species, and the respective percentage coverage was calculated. In the statistical analyses, the mean coverage of the two sampling occasions was used for the coverage of Poaceae and non-Poaceae whereas the sum of coverage values was used for the insect-pollinated plants in flower. Before the analyses, the classes used in the field were transformed into the mean coverage values for each class: $1 = 0.0625\%$, $2 = 0.3125\%$, $3 = 1.25\%$, $4 = 3\%$, $5 = 6\%$, $6 = 12\%$, $7 = 24\%$, $8 = 48\%$ and $9 = 82\%$.

STATISTICAL ANALYSES

We built three sets of statistical models to analyse the patterns of pollinator succession in the experimental study plots and to compare them with surrounding field margins, using the entire 6-year data set. The first two sets of models focused on the patterns of species richness and abundance in bumblebees and diurnal Lepidoptera, whereas the third set of models focused on the abundance patterns of species groups holding different species traits. All analyses were conducted using the program SAS 9.1 (SAS Institute Inc., Cary, NC, USA).

In the first set of analyses, we examined pollinator succession patterns on the set-aside. We built a linear mixed model (LMM) separately for each pollinator response variable: species richness and abundance of bumblebees, butterflies and diurnal moths (all logN + 1-transformed). Seed mixture and mowing were included as fixed explanatory factors and the study year as a continuous covariate in the LMMs. In addition, all the pairwise interactions of these three variables were included to test whether the effects of the seed mixture and mowing varied during vegetation succession in set-aside, as well as whether the effect of the seed mixture varied according to the mowing treatment (or vice versa). The replicate block ($n = 4$, see Appendix S1, Supporting Information) was always included as a random factor. Furthermore, we made pairwise comparisons of the three seed mixtures, based on the differences of least square means (LSMEANS option in SAS). This allowed us to indicate the ranking of the seed mixtures in terms of pollinator species richness and abundance.

In the second set of analyses, we examined the differences in pollinator occurrence patterns between set-aside and surrounding field margins by building linear models. In these models, all the 24 set-aside plots were treated as replicates of the set-aside habitat and the 10 field margins as replicates of the field margin habitat. The models were built separately for each pollinator variable (see earlier). The explanatory variables were the habitat type, the study year and the interaction between these two. Study year was treated as a covariate and habitat type as a categorical variable. The interaction term allowed us to test whether species richness and abundance developed differently in the two habitat types during the 6 study years.

In the third set of analyses, we examined the role of species traits in the succession of pollinator communities on set-aside. We studied one species trait (tongue length) for bumblebees and three traits (larval specificity, larval host plant type and adult mobility) for butterflies and diurnal moths (see Appendix S2 in Supporting Information for species-specific trait information). First response variables were formed for the abundance (logN + 1-transformed) of bumblebees, butterflies and diurnal moths within each category of the focal trait observed in a particular study plot and year. This resulted in two (tongue length, larval specificity and mobility) or four (larval host plant type) repeated measures on each study plot. Then, a separate LMM for each studied species trait was built. When presenting the results of these models, we focus on the interaction between the categorical trait variable and the study year, even though all the same variables as in the first set of analyses were included in these LMMs.

ADDITIONAL ANALYSES

In addition to the main statistical analyses described previously, we conducted a series of complementary analyses to aid the interpretation of the main results. Here, we briefly describe the aims of these analyses, the methods and results of which are presented in Appendices S3–S5 (Supporting Information) in greater detail.

1. Canonical correspondence analyses (CCA; Appendix S3, Supporting Information) were carried out separately for the bumblebees and diurnal Lepidoptera to analyse the relative roles of vegetation characteristics and set-aside age in the succession of pollinator communities on the set-aside.

2. Detrended correspondence analyses (DCA; Appendix S4, Supporting Information) were carried out separately for the bumblebees and diurnal Lepidoptera to compare the succession patterns of pollinator communities on the set-aside and surrounding field margins. DCA was further complemented by an indicator species analysis. This analysis reveals whether a pollinator species shows an indicator value for either set-aside or field margins (Appendix S4, Supporting Information).

3. The occurrence of spatial autocorrelation in pollinator species richness and abundance patterns within the experimental set-aside field was tested following the method used by Heikkinen *et al.* (2005) (Appendix S5, Supporting Information). First, an annual, plot-

specific autocovariate measure for each of the six pollinator variables was calculated, based on the variation of species richness and abundance in all the other study plots. Simple linear correlations were then calculated between each pollinator variable and the corresponding autocovariate measure.

Results

In the set-aside plots, a total of 63 pollinator species and 12230 individuals were observed during the 6 years of the experiment. These included 12 species and 6013 individuals of bumblebees, 21 species and 2761 individuals of butterflies, and 30 species and 3456 individuals of diurnal moths. On the field margins, the total was 71 species and 3646 individuals. These included 11 species and 379 individuals of bumblebees, 25 species and 2122 individuals of butterflies, and 35 species and 1145 individuals of diurnal moths.

SUCCESSION OF SPECIES RICHNESS AND ABUNDANCE ON SET-ASIDE

The sown seed mixture significantly affected bumblebee species richness and abundance, and moth species richness (Table 1, Fig. 1). The pairwise comparisons of the seed mixtures showed that the diverse mixture outperformed the standard mixture in the species richness and abundance of bumblebees and diurnal moths (Table 2). The less competitive mixture was outperformed by the diverse mixture in the same variables, with the exception of moth abundance. The seed mixture-by-year interaction was highly significant in bumblebee variables and significant in moth species richness (Table 1). This was largely because of the increasing relative importance of the standard and less competitive mixtures in comparison with the diverse mixture towards the end of the experiment (Fig. 1). No effect of the mowing treatment or its interaction either with seed mix-

ture or with year on either bumblebees or Lepidoptera was detected. Finally, we found no year effect on bumblebee variables, but a very strong and a highly significant effect on lepidopteran variables (Table 1).

All statistically significant correlations between the pollinator variables and the autocovariate were negative (Appendix S5, Supporting Information), indicating that a high pollinator species richness (or abundance) in the focal plots had a negative effect on pollinator species richness (or abundance) in the surrounding plots.

FACTORS EXPLAINING POLLINATOR OCCURRENCE PATTERNS

Pollinator communities on set-aside were distinctly different at the beginning and at the end of the experiment. In CCA ordinations (Appendix S3, Supporting Information), the study year explained most (70·6%) of the explainable variation in the composition of Lepidoptera and a large percentage (29·0%) in the composition of bumblebee communities. Other statistically significant variables in bumblebees were the coverage of Poaceae, coverage of non-Poaceae and species richness of insect-pollinated plants in flower, whereas in diurnal Lepidoptera the corresponding variables were the coverage of Poaceae and coverage of insect-pollinated plants in flower. In bumblebees, the forward selection procedure (Appendix S3, Supporting Information) eliminated the coverage of insect-pollinated plants in flower because of its strong correlation with the coverage of non-Poaceae.

The identity of the most often visited flowering plants changed during vegetation succession. The five most often visited nectar and pollen plants were *Phacelia tanacetifolia*, *Vicia cracca*, *Centaurea jacea*, *Vicia villosa* and *Cirsium arvense* (Appendix S6, Supporting Information), the former two being

Table 1. Linear mixed model results of the effects of the experimental treatments and the study year on pollinator species richness and abundance (Type III SS)

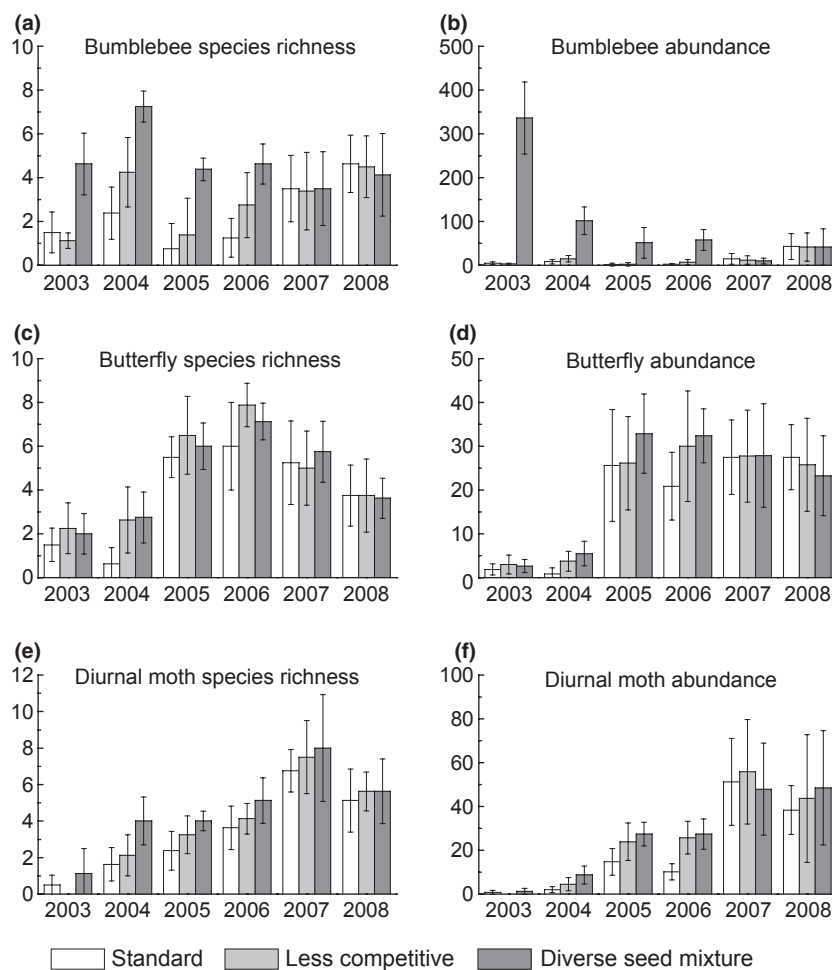|	d.f.	Species richness			Abundance		
		Bumblebees	Butterflies	Diurnal moths	Bumblebees	Butterflies	Diurnal moths
Seed mixture	2	$F = 25·14$ $P = 0·0012**$	$F = 4·16$ $P = 0·0737$	$F = 8·83$ $P = 0·0163*$	$F = 77·93$ $P < 0·0001***$	$F = 4·02$ $P = 0·0781$	$F = 4·48$ $P = 0·0644$
Mowing	1	$F = 0·02$ $P = 0·8923$	$F = 1·59$ $P = 0·2970$	$F = 2·32$ $P = 0·2249$	$F = 0·38$ $P = 0·5833$	$F = 0·47$ $P = 0·5409$	$F = 0·57$ $P = 0·5056$
Year	1	$F = 9·53$ $P = 0·0539$	$F = 39·71$ $P = 0·0081**$	$F = 265·04$ $P = 0·0005***$	$F = 0·31$ $P = 0·6185$	$F = 167·70$ $P = 0·0010**$	$F = 378·21$ $P = 0·0003***$
Seed mixture*Mowing	2	$F = 0·44$ $P = 0·6427$	$F = 0·29$ $P = 0·7523$	$F = 0·85$ $P = 0·4311$	$F = 0·32$ $P = 0·7258$	$F = 0·12$ $P = 0·8911$	$F = 0·95$ $P = 0·3888$
Seed mixture*Year	2	$F = 10·20$ $P < 0·0001***$	$F = 1·84$ $P = 0·1631$	$F = 4·02$ $P = 0·0204*$	$F = 35·43$ $P < 0·0001***$	$F = 2·00$ $P = 0·1401$	$F = 1·61$ $P = 0·2033$
Mowing*Year	1	$F = 0·00$ $P = 0·9782$	$F = 1·31$ $P = 0·2545$	$F = 0·95$ $P = 0·3320$	$F = 0·22$ $P = 0·6373$	$F = 0·25$ $P = 0·6203$	$F = 0·31$ $P = 0·5765$
AIC		221·8	232·4	162·5	426·0	344·5	325·0

$*P < 0·05$, $**P < 0·01$, $***P < 0·001$.

Fig. 1. Responses of species richness and abundance to the three different seed mixtures: the mean number of species per transect (±SD) of (a) bumblebees (c) butterflies and (e) diurnal moths and the mean number of individuals per transect (±SD) of (b) bumblebees, (d) butterflies and (f) diurnal moths.

Table 2. Pairwise comparisons of the three different seed mixtures in the set-aside experiment

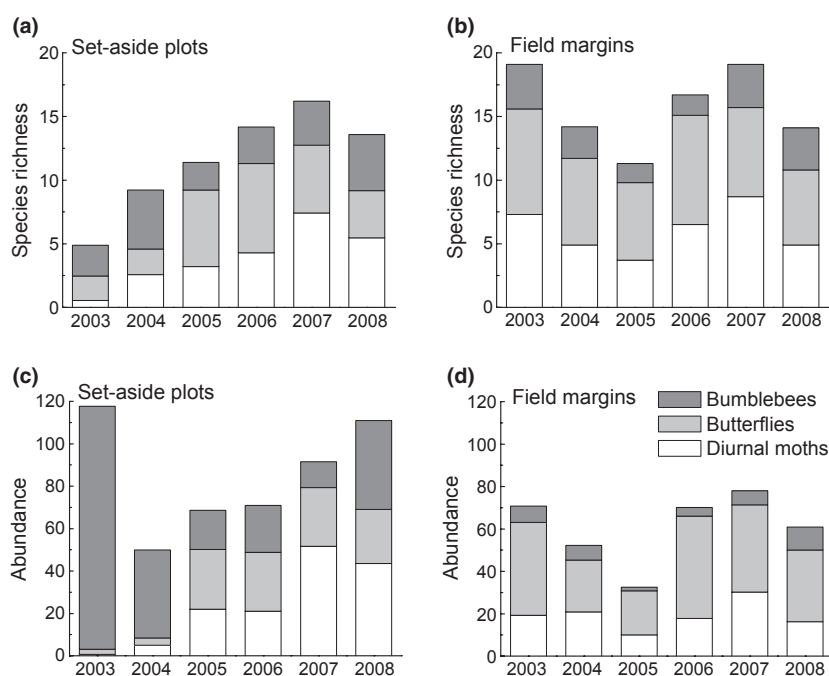|	d.f.	Species richness			Abundance		
		Bumblebees	Butterflies	Diurnal moths	Bumblebees	Butterflies	Diurnal moths
Less competitive vs. standard	6	$t = -1.81$ $P = 0.1201$	$t = -2.25$ $P = 0.0651$	$t = -0.82$ $P = 0.4413$	$t = -1.80$ $P = 0.1211$	$t = -1.61$ $P = 0.1579$	$t = -0.89$ $P = 0.4099$
Diverse vs. standard	6	$t = -6.73$ $P = 0.0005$***	$t = -2.35$ $P = 0.0570$	$t = -3.98$ $P = 0.0073$**	$t = -3.61$ $P = 0.0122$*	$t = -2.32$ $P = 0.0596$	$t = -10.13$ $P < 0.0001$***
Diverse vs. less competitive	6	$t = -4.91$ $P = 0.0027$**	$t = -0.10$ $P = 0.9264$	$t = -3.16$ $P = 0.0197$*	$t = -9.24$ $P < 0.0001$***	$t = -0.71$ $P = 0.5070$	$t = -1.81$ $P = 0.1211$

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

available only during the first 2 years of the experiment. *Phacelia tanacetifolia* is an annual crop plant and *V. villosa* flowers during the second summer after establishment. From the third study year onwards, the most often visited species were perennials, of which *C. jacea* was sown in the diverse mixture, while *C. arvense*, *V. cracca* and *L. pratensis* established naturally. The proportion of flower-visitors among the insect groups was highly variable: a total of 1·6% of the moths, 18·2% of the butterflies and 95·0% of the bumblebees were observed visiting flowers.

COMPARISON WITH FIELD MARGINS

Pollinator species richness and abundance differed significantly between the habitat types, with the only exception being bumblebee species richness (Table 3). The effects of the study year and habitat-by-year interaction on lepidopteran variables were highly significant. The latter result indicates that because of the gradual colonization of set-aside by the butterflies and diurnal moths, the relative importance of the two habitat types changed substantially in the course of the experiment.

Table 3. Linear model results of the effects of the habitat type (set-aside or field margin) and the study year on pollinator species richness and abundance (Type III SS)

	d.f.	Species richness			Abundance		
		Bumblebees	Butterflies	Diurnal moths	Bumblebees	Butterflies	Diurnal moths
Habitat	1	$F = 0.07$ $P = 0.7897$	$F = 53.17$ $P < 0.0001^{***}$	$F = 109.63$ $P < 0.0001^{***}$	$F = 4.21$ $P = 0.0414^{*}$	$F = 98.22$ $P < 0.0001^{***}$	$F = 99.93$ $P < 0.0001^{***}$
Year	1	$F = 3.24$ $P = 0.0728$	$F = 9.14$ $P = 0.0028^{**}$	$F = 56.33$ $P < 0.0001^{***}$	$F = 0.33$ $P = 0.5672$	$F = 54.34$ $P < 0.0001^{***}$	$F = 95.18$ $P < 0.0001^{***}$
Habitat*Year	1	$F = 1.21$ $P = 0.2728$	$F = 19.95$ $P < 0.0001^{***}$	$F = 69.69$ $P < 0.0001^{***}$	$F = 0.02$ $P = 0.8943$	$F = 52.87$ $P < 0.0001^{***}$	$F = 106.71$ $P < 0.0001^{***}$

$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Fig. 2. Responses of species richness and abundance to the experimental set-aside and surrounding field margins: the mean number species (a, b) and individuals (c, d) per transect on the set-aside (a, c) ($n = 24$) and field margins (b and d) ($n = 10$).

Species richness and abundance of pollinators constantly increased on set-aside, while no signs of a systematic trend were detected on the field margins (Fig. 2). Bumblebees were systematically more abundant on the set-aside than on field margins. In butterflies, neither species richness nor abundance permanently reached the levels of the field margins during the entire experiment. Diurnal moths showed a slower response than the butterflies, their species richness increasing until the fifth year of the experiment. Their abundance, in contrast to butterflies, had reached a higher level on the set-aside in comparison with the field margins by the end of the experiment.

In DCA ordinations (Appendix S4, Supporting Information), pollinator communities on the 24 set-aside plots clearly became more similar to each other during succession especially in diurnal Lepidoptera. At the same time, community composition approached that of the field margins but nonetheless remained typical of set-aside. Some pollinator species showed an indicator value ($P < 0.1$) either for set-aside (both in bum-blebees and in Lepidoptera) (e.g. *Bombus lucorum*, *Nymphalis io* and *Scotopteryx chenopodiata*) or for field margins (only in Lepidoptera) (e.g. *Brenthis ino* and *Odezia atrata*).

Table 4. Linear mixed model results of interaction effects between species trait and study year on pollinator abundance (Type III SS) ($^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$)

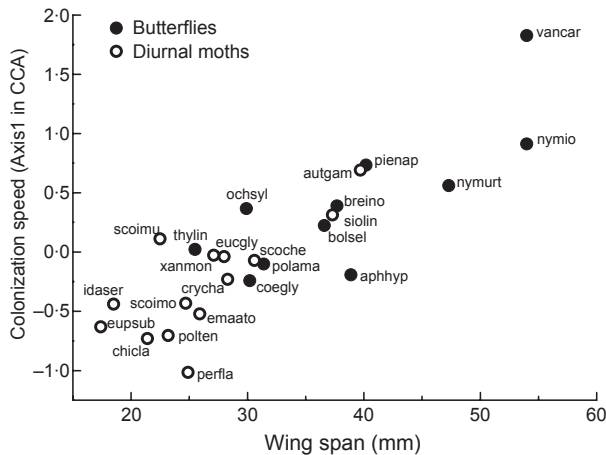|	d.f.	F	P	AIC
Bumblebees				
Tongue length	1	16.78	$<0.0001^{***}$	859.4
Butterflies				
Larval specificity	1	78.20	$<0.0001^{***}$	737.4
Host plant type	3	83.66	$<0.0001^{***}$	1206.3
Mobility	1	1.23	$=0.2687$	667.6
Diurnal moths				
Larval specificity	1	48.93	$<0.0001^{***}$	630.0
Host plant type	3	139.22	$<0.0001^{***}$	947.6
Mobility	1	0.23	$=0.6317$	626.2

Fig. 3. Colonization speed of lepidopteran species on the set-aside in relation to their wing span ($r_p = 0.80$, $P < 0.0001$ for all species; $r_p = 0.73$, $P = 0.01$ for butterflies and $r_p = 0.64$, $P = 0.01$ for diurnal moths).

ROLE OF SPECIES TRAITS IN COMMUNITY ASSEMBLY

Both niche breadth and mobility were found to significantly affect the pattern of pollinator community succession on the set-aside (Table 4, Fig. 3). Niche breadth in bumblebees became narrower as the percentage of the more specialized long-tongued individuals increased during succession (Appendix S7, Supporting Information). In the LMM, this change caused a highly significant interaction between tongue length and study year (Table 4). In diurnal Lepidoptera, both larval specificity and the host plant type interacted highly significantly with the study year (Table 4). In butterflies, this was caused by an increase in the abundance of polyphagous individuals in the former case and by a strong increase in grass-feeding individuals in the latter (Appendix S7, Supporting Information). In diurnal moths, in contrast to butterflies, the percentage of mono- and oligophagous individuals increased during succession. In addition, the proportion of diurnal moth individuals feeding on leguminous plants (family Fabaceae) was increased (Appendix S7, Supporting Information).

In contrast to our expectations, the relative abundance of small (less mobile) lepidopteran individuals did not increase significantly during succession, as we found no significant interaction between the wing span class and study year (Table 4, Appendix S7, Supporting Information). However, a further analysis at species level revealed a clear pattern. We found a strong and significant correlation between the colonization speed (see Appendix S3, Supporting Information for the details of this measure) and the actual wing span (in mm), both in butterflies and diurnal moths (Fig. 3). The larger the species, the faster it colonized the set-aside plots. Furthermore, colonization speed was significantly higher in butterflies than in diurnal moths ($t = 3.18$, $P = 0.0042$, d.f. = 23), because the former group included larger species on average.

Discussion

The studied pollinator groups (bumblebees and diurnal Lepidoptera) differed distinctly in their ability to utilize newly established habitat patches. The observed pattern appears to be closely related to the fundamental ecological differences between the groups, which led them to partially respond to different vegetation characteristics. Furthermore, pollinator responses were associated with niche breadth and dispersal ability within the studied groups.

SUCCESSION OF POLLINATOR COMMUNITIES

Bumblebees responded to available nectar and pollen resources, and their abundance on the set-aside peaked during the first year of the experiment. As our study field was located in a relatively intensively cultivated area, this quick response might simply have been caused by a temporal concentration of foragers on the few resource-rich patches in the landscape (Kleijn & Van Langevelde 2006; Heard *et al.* 2007). Nests were probably mainly located elsewhere and we cannot estimate whether colony reproduction was actually promoted. However, our results support the suggestion that the negative effects caused by the fragmentation of bee habitats can be mitigated by cultivating suitable foraging plants in temporal habitats (Banaszak 1992; Westphal, Steffan-Dewenter & Tscharntke 2003; but see Diekötter *et al.* 2009).

Lepidopteran species richness and abundance were probably more limited by the occurrence of suitable larval host plants as well as the dispersal ability of potential colonizing species. The detailed analysis of the composition of lepidopteran communities supported this interpretation. In butterflies, grass-feeding species were the most successful colonizers. The increasing trend in the abundance of polyphagous butterfly species, which was opposite to our expectations, can also be partly attributed to the growing populations of *Thymelicus lineola* and *Aphantopus hyperantus* on the set-aside. Both of these abundant, grass-feeding species were classified as polyphagous in their larval specificity. In diurnal moths, several species feeding on leguminous plants (e.g. *Scotopteryx chenopodiata*, *Chiasmia clathrata* and *Euclidia glyphica*) seem to have successfully established populations on the experimental plots. The percentage of these species even exceeded the level recorded on the field margins during succession.

Furthermore, small and therefore less mobile lepidopteran species colonized the set-aside plots more slowly than large and more mobile species. Diurnal moths were on average slower colonizers than butterflies, which can probably be explained by their smaller average size. These results support the findings of several recent studies on farmland biodiversity, which have reported that community level responses to both habitat loss (Ekroos, Heliölä & Kuussaari 2010; Öckinger *et al.* 2010) and habitat management (Merckx *et al.* 2010) are significantly affected by varying mobility between species.

SIGNIFICANCE OF THE SOWN SEED MIXTURE

As expected, the use of alternative seed mixtures benefited the pollinators, with significant effects observed in bumblebees and diurnal moths. The superiority of the diverse mixture, which contained several nectar and pollen plants, was especially evident in the bumblebees during the first year of the experiment. Short-tongued bumblebees were very abundant in the year of establishment on *Phacelia tanacetifolia*, a plant with a widely recognized agronomic and ecological value (Carreck & Williams 2002). Subsequently, *Vicia villosa* and *Centaurea jacea* contributed significantly to nectar and pollen availability in the plots sown with this seed mixture. The former species has a long corolla tube and is therefore suitable for long-tongued bumblebees. The latter species was unfortunately not in full bloom during the field surveys in the last two study years, which partly explains the apparent decreasing value of the diverse mixture in comparison with the other two mixtures towards the end of the experiment.

The most often visited plants that established naturally were *Cirsium arvense*, *Vicia cracca* and *Lathyrus pratensis*. The number of flower visits to the first species peaked during the third study year and visits to the last two species peaked during the sixth study year; thus, it took several years before other important nectar and pollen plants became available in addition to the sown species. These results are in agreement with earlier studies, which indicate that pollinator populations can be enhanced by sowing well chosen plant species. This is useful for overcoming the small seedbank of arable fields, speeding up the availability of plant species that are late colonizers in natural succession (Smith *et al.* 2002; Öster *et al.* 2009) and improving the availability of nectar and pollen sources.

IMPLICATIONS FOR MAINTAINING AND ENHANCING POLLINATOR DIVERSITY

Halting biodiversity loss and enhancing the value of agricultural landscapes require effective practical measures, developed through carefully designed field experiments. In an ideal situation, pollinators thriving in extensively managed areas such as set-aside could also provide pollination services on surrounding, intensively managed farmland (Albrecht *et al.* 2007; but see Kohler *et al.* 2008). Another wider benefit of set-aside could be the softening of agricultural matrix, because of increased habitat connectivity (Donald & Evans 2006). This could be of particular benefit to the more specialized and less mobile species, which have suffered from agricultural intensification the most (Ekroos, Heliölä & Kuussaari 2010).

When set-aside at different stages of vegetation succession is included in the landscape, it is likely that the needs of a wide variety of organisms will be met. A prerequisite for attracting bumblebees to set-aside is the sowing of suitable nectar and pollen plants. In diurnal Lepidoptera, other key features of the vegetation include a high coverage of both Poaceae and Fabaceae. More importantly, a set-aside duration of at least 5 years is recommendable when aiming to enhance lepidopteran populations.

Long-term set-aside can be supported through agri-environment schemes (Berger, Kaechele & Pfeffer 2006), which should be both ecologically sound and cost-effective (Whittingham 2011). In these schemes, the payment for farmers needs to be high enough to compensate for the loss of income and to cover the expense of set-aside establishment and management. In addition, the availability of nectar and pollen plant seeds as well as seeds of less competitive grasses may need to be economically supported.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Spatial study design of the set-aside experiment.

Appendix S2. Species list of pollinators and their species traits.

Appendix S3. CCA ordination methods and results.

Appendix S4. DCA ordination methods and results.

Appendix S5. Autocorrelation effects in the experiment.

Appendix S6. Pollinator flower visits on the set-aside plots.

Appendix S7. Succession of pollinator communities according to species traits.

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