

Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries

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Summary

1. Growing evidence for declines in wild bees calls for the development and implementation of effective mitigation measures. Enhancing floral resources is a widely accepted measure for promoting bees in agricultural landscapes, but effectiveness varies considerably between landscapes and regions. We hypothesize that this variation is mainly driven by a combination of the direct effects of measures on local floral resources and the availability of floral resources in the surrounding landscape.

2. To test this, we established wildflower strips in four European countries, using the same seed mixture of forage plants specifically targeted at bees. We used a before–after control–impact approach to analyse the impacts of wildflower strips on bumblebees, solitary bees and Red List species and examined to what extent effects were affected by local and landscape-wide floral resource availability, land-use intensity and landscape complexity.

3. Wildflower strips generally enhanced local bee abundance and richness, including Red-listed species. Effectiveness of the wildflower strips increased with the local contrast in flower richness created by the strips and furthermore depended on the availability of floral resources in the surrounding landscape, with different patterns for solitary bees and bumblebees. Effects on solitary bees appeared to decrease with increasing amount of late-season alternative floral resources in the landscape, whereas effects on bumblebees increased with increasing early-season landscape-wide floral resource availability.

4. *Synthesis and applications.* Our study shows that the effects of wildflower strips on bees are largely driven by the extent to which local flower richness is increased. The effectiveness of this measure could therefore be enhanced by maximizing the number of bee forage species in seed mixtures, and by management regimes that effectively maintain flower richness in the strips through the years. In addition, for bumblebees specifically, our study highlights the importance of a continuous supply of food resources throughout the season. Measures that enhance early-season landscape-wide floral resource availability, such as the cultivation of oil-seed rape, can benefit bumblebees by providing the essential resources for colony establishment and growth in spring. Further research is required to determine whether, and under what conditions, wildflower strips result in actual population-level effects.

Key-words: agri-environment, ecosystem services, field boundaries, floral resources, flower strips, landscape context, pollinators

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Introduction

Flower-visiting insects such as wild bees provide essential pollination services to both crops and wild plants (Ollerton, Winfree & Tarrant 2011; Garibaldi *et al.* 2013). However, reported declines of wild bee richness and abundance (Biesmeijer *et al.* 2006; Kosior *et al.* 2007) have raised concerns about potential pollination deficits (Garibaldi *et al.* 2013) and increased the urgency to develop and implement effective measures mitigating wild bee decline. Loss of floral resources, largely driven by expansion and intensification of agriculture, is one of the main drivers of wild bee decline (Scheper *et al.* 2014). Concomitantly, current actions to mitigate bee decline often aim to enhance floral resources (Winfree 2010), either directly (e.g. by sowing wildflowers) or indirectly (e.g. by extending agricultural practices). While most of these actions result in higher bee abundance and diversity, there is considerable variation in the magnitude of effects among initiatives, with effectiveness differing among different types of measures and varying across landscapes and regions (Kleijn *et al.* 2006; Scheper *et al.* 2013; Schneider *et al.* 2014). Understanding the causes of this variation may help us more effectively mitigate loss of wild bees.

Local bee abundance and species richness are generally positively correlated with flower cover and richness (Potts *et al.* 2003), and effects of current mitigation measures appear to be predominantly operating through effects on floral resource availability (e.g. Pywell *et al.* 2006; Holzschuh *et al.* 2007). Variation in effectiveness of different measures may thus be mainly explained by the extent to which measures improve local floral resource availability compared to conventionally managed habitats (Scheper *et al.* 2013), that is the extent to which measures create an ecological contrast, *sensu* Kleijn *et al.* (2011). Additionally, bee responses to mitigation measures not only depend on effects of measures on local floral resources but are also affected by composition of the landscape (e.g. farmland type, proportion of semi-natural habitat; Scheper *et al.* 2013). The same measure may thereby have varying effects depending on the region-specific landscape contexts (Holzschuh *et al.* 2007; Carvell *et al.* 2011; Schneider *et al.* 2014). The influence of landscape context on effectiveness of mitigation measures may mainly operate through effects of landscape-wide floral resource availability (Carvell *et al.* 2011). However, it remains unknown to what extent local and landscape-scale resources determine bee responses to mitigation measures, how important these are compared to other environmental factors, and whether responses differ between species groups.

So far, studies that have examined the effects of mitigation measures on wild bees have not included baseline measurements of bee richness and abundance. Comparisons between treatment and control sites in such studies therefore cannot distinguish between initial site differences and differences induced by the measures. This may bias

results if measures are for instance located on less productive fields that already support higher levels of biodiversity (Kleijn & Sutherland 2003). Examining the effectiveness of measures should therefore be done by comparing bee trends on sown flower strips and control sites both before and after implementation of the measures (before–after control–impact (BACI) design) (Kleijn *et al.* 2006). Furthermore, if treatment and control sites are located in spatially independent landscapes and bee responses are monitored over multiple years after implementation, such a design may allow disentangling small-scale spatio-temporal foraging responses from actual population-level responses (Kleijn *et al.* 2011). To our knowledge, studies that have thus far evaluated measures to support bees have not used such an approach.

Here, we test whether we can explain the response to mitigation measures of bumblebees and solitary bees by means of changes in floral resources and the characteristics of the surrounding landscape. In four European countries, we established wildflower strips along field boundaries in agricultural landscapes along a gradient of land-use intensity, proportion of semi-natural habitat and landscape-wide floral resource availability. In each country, we used the same seed mixture, allowing us to systematically investigate the relative importance of the different environmental factors in explaining the effectiveness of the wildflower strips. Initial between-site differences were taken into account by using a 3-year BACI design to compare bumblebee and solitary bee abundance and richness between wildflower strips and control field boundaries located in spatially independent landscapes. The specific research questions we addressed were as follows: (i) whether the effects of wildflower strips on bees differ between countries and species groups; (ii) whether the magnitude of the effects of wildflower strips can be explained by local and landscape-level floral resources or other environmental factors; and (iii) whether the importance of environmental factors differs between bumblebees and solitary bees. We furthermore discuss to what extent our results point towards population-level effects of wildflower strips or mainly indicate foraging responses. Answers to these questions will help us design more effective mitigation measures.

Materials and methods

EXPERIMENTAL DESIGN

The experiment was conducted from 2011 to 2013 in Germany, Sweden, the Netherlands and the United Kingdom. In each country, we selected eight 'pre-treatment' field boundaries, where at the end of the first study year, wildflower strips were to be established alongside. Another eight field boundaries were selected to serve as control sites. All field boundaries were adjacent to conventionally managed arable fields and were located at least 2 km apart, in different landscapes (1-km radius around field boundaries), to ensure spatial independence among sites given the

predominant flight ranges of wild bees (Zurbuchen *et al.* 2010). The conventionally managed field boundaries were dominated by grasses and were generally mown 1–3 times per year without removal of the cut vegetation. Care was taken to ensure that landscapes surrounding the treatment and control sites covered similar gradients in land-use intensity (annual nitrogen input per hectare of agricultural land in the landscape), landscape complexity (percentage semi-natural habitat) and landscape-wide floral resource availability (see section ‘Quantifying Landscape Characteristics’ below). In all countries except the UK, means for landscape context variables were similar for treatment and control landscapes (Table S1, Supporting Information). Due to time constraints, study site selection in the UK was more *ad hoc*, unfortunately resulting in differences in the proportion of semi-natural habitat ($t_{(12)} = 4.03$, $P = 0.002$) and early-season floral resource availability ($t_{(12)} = -3.64$, $P = 0.003$) between treatment and control sites. Across countries, landscape variables were only weakly correlated (all $|r| < 0.32$).

In the autumn of 2011, we established wildflower strips alongside pre-treatment field boundaries. Strips (100 × 3 m) were sown with a seed mixture (2 g m⁻²) of mid- to late-season flowering plants attractive to bees, based on expert opinion. In each country, seeds of local provenance were used. The mixture was composed of *Borago officinalis* (8% of the seeds), *Centaurea jacea* (8%), *Foeniculum vulgare* (8%), *Hypericum perforatum* (15%), *Hypochaeris radicata* (12%), *Leontodon hispidus* (13%), *Malva sylvestris* (8%), *Papaver rhoeas* (8%), *Pastinaca sativa* (8%), *Tanacetum vulgare* (4%), *Trifolium pratense* (4%) and *Trifolium repens* (4%). These robust species commonly occur in each of the four countries and can establish on a wide variety of soils. Flower strips were not fertilized or managed during the 2 years after their establishment.

SURVEYING BEES AND FLOWERING PLANTS

In 2011, control and pre-treatment field boundaries were surveyed for baseline data on wild bees (i.e. excluding the managed honeybee *Apis mellifera*) and flowering forbs. In 2012 and 2013, bees and plants were surveyed in the newly established wildflower strips and control field boundaries. Surveys were carried out twice every year during the flowering period of the sown plant species: once in June and once in the period from mid-July to the end of August. Five sites in 2011 (two control and three pre-treatment field boundaries) and two sites in 2012 (both flower strips) were surveyed only once. We could not collect baseline data for one flower strip site in the UK because the land owner did not participate in the study until autumn 2011. Another flower strip site in the UK was flooded and failed to establish, and this site was therefore excluded from the analysis.

We sampled bees using standardized transect walks in two contiguous 150 m² transects (15 min pure collecting time per transect) and recorded flower cover and species richness of flowering forb species in each transect. All forb species in the transect flowering at the time of the survey were recorded and identified to species level. For each recorded forb species, the total cover of its flowers was calculated as the total number of flower units × the mean surface area of the flower unit, divided by the transect area. Dimensions of transects in wildflower strips were 50 × 3 m; dimensions of transects in control field boundaries varied according to the size of the field boundaries, with widths ranging between 1 and 3 m. Surveys were carried out between 9.00 and

18.00 h on days with dry weather, low wind speeds and temperatures above 15 °C. Bees that could not be identified to species on the wing were collected and identified in the laboratory; bees that could not be caught were described in best possible taxonomic detail.

QUANTIFYING LANDSCAPE CHARACTERISTICS

Land-use intensity in study landscapes was calculated as nitrogen input per hectare of agricultural land per year. Nitrogen input generally correlates with other farming intensity measures (e.g. yield, pesticide use, density of livestock units) and is commonly used as a key indicator for land-use intensity (Herzog *et al.* 2006). Data on nitrogen input in each study landscape were acquired from farmers using questionnaires on fertilizer use. Management data were obtained from farms covering at least 30% of the agricultural land in the study landscape.

Landscape composition was determined using national topographical maps and aerial photographs, validated by field inspections. We used ArcMap 10 (ESRI, Redlands, CA, USA) to calculate the relative cover of the land-use types in each landscape and quantified landscape complexity as the proportion of semi-natural habitat suitable as foraging and nesting sites for bees (e.g. forest edges, semi-natural grasslands, hedges, heathlands, orchard meadows) (Tscharntke *et al.* 2005). We used a stratified sampling approach (see Appendix S1 for methods) to determine the landscape-wide floral resource availability, both before (in May) and during (in July–August) peak flowering of the wildflower strips. The rationale for assessing resource availability before peak flowering of the strips is that responses of bees to late-season-enhanced flower supply may be affected by early-season resource availability (Riedinger *et al.* 2014), particularly in the case of bumblebees which have relatively long colony cycles (Williams, Regetz & Kremen 2012).

DATA ANALYSIS

Linear mixed models, with response variables averaged over transects and sampling rounds, were used to examine the effects of wildflower strip establishment on abundance and species richness of bees and flowers. Effects of wildflower strips were analysed for bumblebees and all other wild bees separately. Although some halictid bee species display primitive eusocial behaviour, all bee species other than bumblebees were referred to as ‘solitary bee species’. To improve normality and homoscedasticity of residuals, abundance and species richness of bumblebees and solitary bees were $\ln(x + 1)$ -transformed, and flower cover was logit-transformed.

We first built models containing the fixed factors ‘treatment’ (control vs. pre-treatment or sown flower strip), ‘year’, ‘country’ and all their interactions (up to three-way) to assess whether effects of sown flower strips on flowers, bumblebees and solitary bees differed among countries. Study site was included as a random factor to account for the repeated measures in the BACI design. The statistical significance of the two-way treatment × year interaction indicates whether establishing wildflower strips has effects on flowers and bees, whereas the significance of the three-way treatment × year × country interaction indicates whether the effect of wildflower strips (i.e. the nature and strength of the treatment × year interaction) differs among countries. Next, as significant three-way interactions revealed

differences in patterns among countries, we examined the effects of flower strips for each country separately, using models that included treatment, year and treatment \times year as fixed factors and study site as a random factor. Significance of fixed effects was assessed by comparing models with and without the factor of interest using likelihood ratio tests. For models with significant treatment \times year interactions, we used non-orthogonal contrasts to decompose the interaction into separate treatment \times year interactions for the periods 2011 vs. 2012 and 2012 vs. 2013. Significant positive interactions in both periods would indicate continued enhancement of bees in wildflower strips, which may be indicative of population-level effects.

In supplementary analyses, we evaluated the value of the wildflower strips for species of conservation concern by comparing the abundance and species richness of rare and endangered bee species in wildflower strips and control field boundaries. Conservation status of species was based on National Red Data Books (Appendix S2). Numbers of observed Red List species in control and pre-treatment sites in 2011 were low, with many zero values in Germany and no observations at all in Sweden, the Netherlands and the UK. We therefore restricted the analyses of effects on Red List species to the 2012 and 2013 data only. However, as numbers of observations were also generally low when analysing the data of both years separately, we summed the 2012 and 2013 abundance and species richness of Red List species per site and performed analyses for the combined after-treatment period, for each country separately. Analyses were performed using generalized linear models with Poisson distribution (quasi-poisson in case of overdispersion) and log-link function, using \ln (number of surveyed transects) as an offset to account for missing transects or sampling rounds at some sites.

In a second set of analyses, we investigated whether and to what extent the variation in the magnitude of the effect of wildflower strips among countries and landscapes can be explained by the environmental factors: land-use intensity (N input), landscape complexity (% semi-natural habitat), local change in floral resource availability and landscape-wide floral resource availability. In these analyses, we used the within-site relative change in bee abundance and richness between 2011 and 2013, measured as the log response ratio ($\ln X_{2013}/X_{2011}$, with one added to account for zeros), as response variable. Similarly, the explanatory variable local relative change in floral resource availability was measured as the within-site relative change (\ln response ratio) in flower cover and richness between 2011 and 2013. The variables of landscape-wide floral resources in May (early) and in July–August (late) were \ln transformed prior to analysis to reduce positive skew.

We could not construct a model set including all possible combinations of environmental variables and their interactions due to the limited number of observations and problems with interpreting higher order interactions. We therefore manually constructed a model set consisting of ecologically meaningful models including up to three-way interactions. For each environmental factor, we included separate linear mixed models, with country as random factor, relating the relative change in bees to (i) the environmental factor only; (ii) the additive effect of the environmental factor and treatment; or (iii) the interaction between the environmental factor and treatment (also including both main effects). For the analysis of effects of landscape complexity, we also included a quadratic term, as the relationship between landscape complexity and effectiveness of mitigation measures is hypothe-

sized to be hump-shaped (Tscharntke *et al.* 2005). Intercept-only and treatment-only models were included for reference. To specifically investigate how the effectiveness of wildflower strips depends on the interplay of landscape-wide availability of floral resources and local changes in floral resources, we built models containing all possible combinations of treatment, landscape-wide floral resources and relative change in local flower resources, including their two-way and three-way interactions. This was done for early and late landscape-wide resources separately and for relative change in local flower cover and richness separately. Separate analyses were performed for abundance and richness of bumblebees and solitary bees, with a total of 67 models included in the model set in each analysis.

We used an information-theoretic approach to assess the relative support for the different models in the model set. We ranked models based on their Akaike Information Criterion values corrected for small sample size (AIC_c) and restricted our candidate set to models with $\Delta AIC_c < 2$ (Burnham, Anderson & Huyvaert 2011). Akaike model weights (ω), which reflects the probability that a model is the best approximating model in the candidate set, were calculated for each model in the candidate set. Comparison of the composition of the best models for bumblebees and solitary bees would indicate whether the most important environmental factors are the same for both species groups.

The *ad hoc* study site selection in the UK resulted in systematic differences between treatment and control study sites in terms of percentage of semi-natural habitat and floral resource availability in May (Table S1). To assess whether these systematic differences affected the results on the effects of environmental factors, we performed analyses that included all sites and analyses excluding the most deviating study sites in the UK (control sites with exceptionally high proportion of semi-natural habitat and flower strip sites with exceptionally high early floral resource availability: six sites in total). Although results were similar for bumblebees, results for solitary bees differed between analyses. We therefore present the results of the analyses that excluded the six deviating UK study sites, so that percentage of semi-natural habitat and early floral resource availability were not confounded with treatment. Results of the analysis on the full data set are shown in Table S2.

All analyses were performed using R version 3.1.0 (R Core Team 2014).

Results

FLORAL RESOURCES IN FLOWER STRIPS

A total of 311 species of flowering forbs were recorded. The extent to which sown flower strips enhanced floral resources differed between countries (three-way interaction between treatment, year and country for flower cover $\chi^2_{(6)} = 18.50$, $P = 0.005$ and for flower richness $\chi^2_{(6)} = 40.02$, $P < 0.001$). In Germany and the UK, establishment of wildflowers resulted in enhanced flower cover in the second year after establishment only, mainly due to decreasing flower cover in control sites, whereas in Sweden and the Netherlands, flower cover was enhanced in the first year after establishment and remained constant in the second year (Fig. S1; Table 1; Table S3). Establishment of

Table 1. Results of linear mixed models for interaction effects of treatment and year on flower cover and richness, bumblebee abundance and richness, and solitary bee abundance and richness in each country. Significant treatment \times year interactions are shown in bold

	Germany		Sweden		The Netherlands		UK	
	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
Flowers								
Cover	9.94	0.007	7.73	0.021	21.53	< 0.001	20.64	< 0.001
Species richness	2.93	0.231	29.12	< 0.001	26.77	< 0.001	11.39	0.003
Bumblebees								
Abundance	7.82	0.020	13.71	0.001	18.03	< 0.001	31.34	< 0.001
Species richness	3.63	0.163	4.04	0.133	18.01	< 0.001	27.17	< 0.001
Solitary bees								
Abundance	11.47	0.003	9.91	0.007	7.27	0.026	7.72	0.021
Species richness	6.91	0.032	3.84	0.147	6.52	0.038	7.27	0.026

flower strips had positive effects on flower richness in Sweden, the Netherlands and the UK, but not in Germany (Table 1). In the Netherlands, establishment of wildflower strips increased flower richness in the first year after establishment, but the difference between wildflower strips and control sites decreased in the following year. In Sweden and the UK, effects of flower strips on flower richness only became apparent in the second year after establishment (Fig. S1; Table S3).

EFFECTS OF WILDFLOWER STRIPS ON BEE ABUNDANCE AND SPECIES RICHNESS

In total, 5768 bumblebees and 1405 solitary bees were observed across 3 years. We identified 22 bumblebee species, of which six were Red Listed, and 103 solitary bee species, of which 29 were Red Listed. *Bombus lapidarius* (1686 individuals), *Bombus terrestris/lucorum* complex (1429) and *Bombus pascuorum* (1112) were the most abundant bumblebee species, and *Lasioglossum villosulum* (124), *Lasioglossum pauxillum* (93) and *Heriades truncorum* (79) were the most abundant solitary bees.

The effectiveness of flower strips in increasing bumblebee abundance and species richness (i.e. the strength of the treatment \times year interaction) differed among countries (abundance $\chi^2_{(6)} = 30.93$, $P < 0.001$; species richness $\chi^2_{(6)} = 25.65$, $P < 0.001$). In Germany, wildflower strips enhanced bumblebee abundance in the second, but not in the first year after establishment. In Sweden and the Netherlands, wildflower strips resulted in enhanced bumblebee abundance in 2012, after which the difference between flower strips and control sites remained constant in 2013. The most pronounced effects were observed in the UK, where flower strips resulted in enhanced bumblebee abundance after the first year of establishment and the difference between flower strips and control sites continued to increase in the second year (Fig. 1; Table S3). In the Netherlands and the UK, patterns for bumblebee richness were similar to the patterns for abundance, but contrary to the positive effects of wildflower strips on bumblebee abundance in

Germany and Sweden, no effects on bumblebee richness were observed in these countries (Fig. S2; Tables 1 and S3).

In contrast to the between-country differences for the effects of wildflower strips on bumblebees, the effects on solitary bees were similar among countries (interaction treatment \times year \times country abundance $\chi^2_{(6)} = 4.77$, $P = 0.574$; species richness $\chi^2_{(6)} = 2.33$, $P = 0.887$). The abundance of solitary bees was enhanced by wildflower strips in each country (Table 1) and between-year patterns were similar, with enhanced solitary bee abundance in 2012 and differences between wildflower strips and control field boundaries remaining stable in 2013 (Fig. 1; Table S4). Patterns for solitary bee richness resembled those for solitary bee abundance (Table 1; Fig. S2; Table S3), although the treatment \times year interaction for solitary bee richness was not significant in Sweden. In most countries, effect sizes of flower strips were larger for bumblebees than for solitary bees (Figs 1 and S2).

Overall, very few individuals of Red-listed bee species were observed over the 3-year study period in each country, with the majority of individuals observed in Germany (134), followed by the UK (17), the Netherlands (13) and Sweden (9). After wildflower strip establishment, abundance of Red List bees was higher in wildflower strips than in control field boundaries in all countries except Sweden. Species richness of Red List bee species was only enhanced by flower strips in the UK (Table S4).

ENVIRONMENTAL FACTORS INFLUENCING EFFECTS OF WILDFLOWER STRIPS

Observed relative changes in bumblebee abundance in wildflower strip and control sites between 2011 and 2013 were unequivocally best explained by the model including the local change in flower richness and the interaction between treatment and early-season landscape-wide floral resource availability ($\omega = 1.00$, Table 2). The relative change in bumblebee abundance in sites increased with the relative change in local flower richness between 2011 and 2013, and the absence of an interaction with treatment

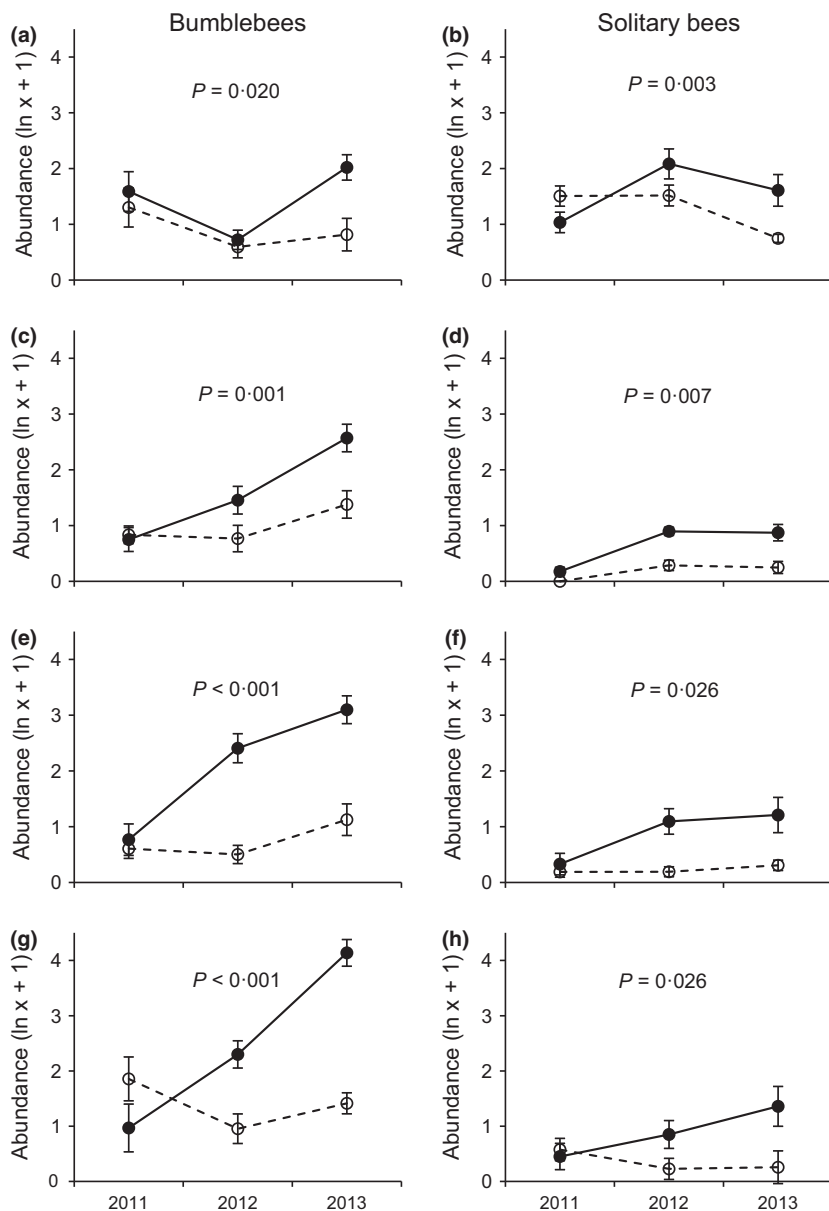


Fig. 1. Mean abundance of bumblebees and solitary bees in wildflower strips (filled circles, solid lines) and control field boundaries (open circles, dashed lines) in Germany (a, b), Sweden (c, d), The Netherlands (e, f) and the UK (g, h). Error bars represent SE. P values indicate significance of the treatment \times year interactions (see Table 2). See Table S3 for significance of the specific treatment \times 2011–2012 and treatment \times 2012–2013 contrasts.

indicates that the strength of this relationship was similar in wildflower strips and control field boundaries (Fig. 2a). Treatment had an additive effect to the general effects of changes in local flower richness, with larger changes in wildflower strips than in control sites. However, the strength of the effect of treatment depended on early-season availability of floral resources in the study landscapes: differences between the magnitude of changes in wildflower strips and control sites increased with increasing early-season landscape-wide cover of floral resources (Fig. 2b). Similar results were observed for bumblebee richness: local change in flower richness and the interaction effects of treatment and early landscape-wide floral resource availability also best explained the changes in bumblebee richness in sites ($\omega = 0.68$, Table 2; Fig S3).

The best model explaining relative changes in solitary bee abundance included the factors local change in flower

richness and the interaction between treatment and late-season landscape-wide floral resource availability ($\omega = 0.36$, Table 2). This model resembled the models for bumblebees with respect to the positive effects of local change in flower richness (Fig. 3a), but the effect of treatment on changes in solitary bee abundance depended on late-season floral resource availability and was negative: differences between wildflower strips and control sites decreased with increasing late-season landscape-wide floral resource availability (Fig. 3b). However, there was considerable uncertainty associated with selection of the best model for changes in solitary bee abundance: the simpler, second best model, which only included the factors treatment and local change in flower richness, performed nearly as good as the best model ($\Delta AIC_c = 0.45$, Table 2). Likewise, for changes in solitary bee richness, the highest ranked model ($\omega = 0.31$), which included the factors

Table 2. Candidate models ($\Delta AIC_c < 2$) explaining the relative change in bee abundance and richness in wildflower strips and control sites between 2011 and 2013

Response variable	Explanatory variable										ω
	T	FR	RES _{Early}	RES _{Late}	N	SNH	T × FR	FR × RES _{Early}	T × RES _{Early}	T × RES _{Late}	
Bumblebees Abundance	1.26	1.00	0.26						1.39		1.00
Richness	0.38	0.69	0.19						0.58		0.68
	0.37	0.66	0.16					0.31	0.48		0.32
Solitary bees Abundance	0.65	0.65		−0.17						−0.76	0.36
	0.71	0.52									0.28
	0.70	0.56					−0.53				0.22
	0.65	0.66		−0.14			−0.36			−0.71	0.14
Richness	0.31	0.25									0.31
	0.41										0.31
	0.31	0.25			0.11		−0.20				0.14
	0.40					0.07					0.13
	0.41										0.11

Models are ranked in order of increasing differences in corrected Akaike Information Criterion (ΔAIC_c). Regression coefficients, standardized by centring and dividing by two SDs, are given for the explanatory variables in each model. Akaike model weights (ω) indicate the probability that a model is the best approximating model in the candidate set. T, treatment (wildflower strip vs. controls site); FR, relative change in local flower richness between 2011 vs. 2013; RES_{Early}, landscape-wide floral resource availability in May; RES_{Late}, landscape-wide floral resource availability in July–August; N, nitrogen input; SNH, proportion semi-natural habitat.

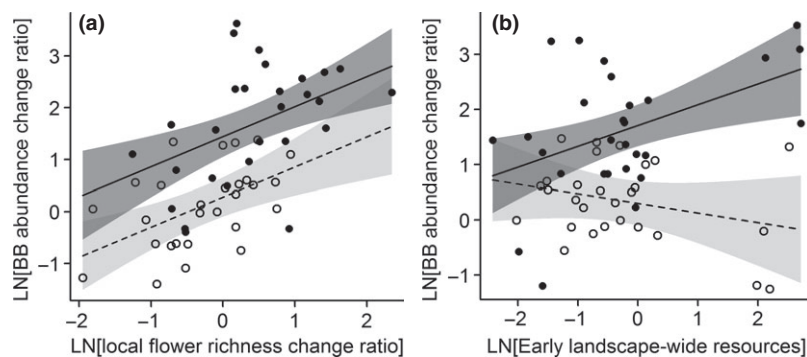


Fig. 2. Conditional partial regression plots for the best model explaining the relative change in bumblebee (BB) abundance between 2011 and 2013 (see Table S2): (a) effects of local relative change in flower richness between 2011 and 2013 and (b) interacting effects of treatment (wildflower strips, filled circles and solid lines; control field boundaries, open circles and dashed lines) and early-season landscape-wide floral resource availability on relative change in BB abundance. Plotted points are partial residuals; shaded areas indicate 95% confidence intervals.

treatment and local change in flower richness, hardly performed better than the second-best treatment-only model ($\Delta AIC_c = 0.004$, Table 2).

Discussion

Our study shows that, although establishing wildflower strips generally enhances local bee abundance and richness including Red-listed species, the magnitude of the effects of flower strips depends on the interplay between the degree of enhancement of local floral resources in the strip and the amount of floral resources in the surrounding landscape. Variation in local and landscape-wide floral resources explained differences between the effect sizes of wildflower strips in four intensively farmed European countries. The modulating effects of landscape-wide floral resource availability differed, however, between species groups: for bumblebees, effects of flower strips increased with increasing early-season landscape-wide floral resource availability (Figs 2 and S3), whereas for solitary bees effects were less clear but appeared to decrease with increasing late-season landscape-wide resource availability (Fig. 3).

Enhanced bee richness and abundance in wildflower strips (Figs 1 and S2) generally reflected the enhancement of both cover and richness of flowering forbs in the strips compared to pre-treatment and control field boundaries (Fig. S1), and between-site differences in the relative increase in bee abundance and richness between 2011 and 2013 were best explained by the extent to which flower richness was increased (Table 2). These findings are in line with the results of a recent meta-analysis in which the effects of agri-environment schemes on bees increased with increasing induced ecological contrast in terms of forb cover and richness between sites with conservation management and control sites (Scheper *et al.* 2013). Furthermore, on top of the general effects of changes in flower richness, establishment of flower strips in itself resulted in higher increases in bee densities and richness than in control field boundaries. This probably points to the added value of the seed mix that was specifically targeted at bees, indicating that the sown plants species in the wildflower strips were more attractive to bees than the plant species generally found in conventional field boundaries. General agri-environmental extensification

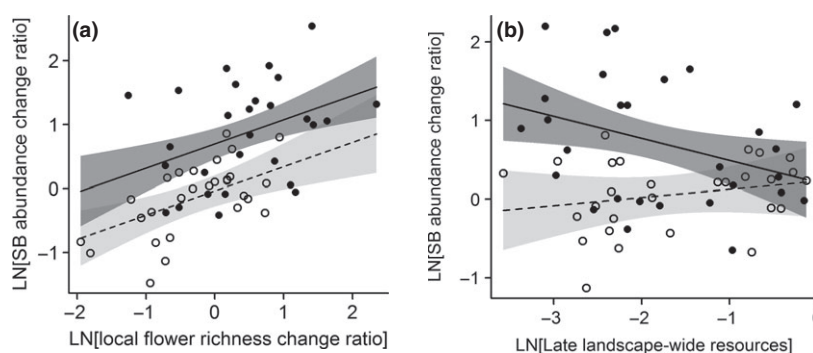


Fig. 3. Conditional partial regression plots for the best model explaining the relative change in solitary bee (SB) abundance between 2011 and 2013 (see Table S2): (a) effects of local relative change in flower richness between 2011 and 2013 and (b) interacting effects of treatment (wildflower strips, filled circles and solid lines; control field boundaries, open circles and dashed lines) and late-season landscape-wide floral resource availability on relative change in SB abundance. Plotted points are partial residuals; shaded areas indicate 95% confidence intervals.

measures, such as conservation headlands, set-asides and grass-sown or naturally regenerated extended-width field margins that are implemented on intensive farmland to create habitats for wildlife, generally promote common bee species (Scheper *et al.* 2013), but they rarely benefit bee species of conservation concern (Kleijn *et al.* 2006). In contrast, and in line with Pywell *et al.* (2012), our study shows that measures that directly enhance floral resources specifically targeted at bees may also promote rare and endangered bee species.

Although there was considerable model selection uncertainty, we found indications that responses of solitary bees to wildflower strips depended, in addition to the local contrast in floral resources, on the landscape-wide availability of floral resources: effects of wildflower strips on solitary bee abundance appeared to decrease with increasing late-season landscape-wide floral resource availability (Fig. 3). This apparent negative modulating effect of late landscape-wide floral resource availability may reflect that flower strips are relatively less attractive in landscapes with high resource availability (small ecological contrast) than in landscapes with low resource availability (large ecological contrast). Consequently, in landscapes with low availability of alternative floral resources, bees may display stronger concentration responses on the wildflower strips (Carvell *et al.* 2011), whereas in resource-rich landscapes, foraging bees may be expected to be more evenly distributed over the landscape and display more diluted patterns (Veddeler, Klein & Tschardt 2006; Holzschuh *et al.* 2011). The enhancement of solitary bee abundance by wildflower strips did not depend on early landscape-wide resource availability. Most solitary bees in the wildflower strips and control field boundaries were univoltine species, and many of these are active for only a few weeks. The solitary bees observed during the two survey rounds in June and July–August were therefore unlikely to be affected by landscape-wide floral resources availability in May.

Conversely, effects of wildflower strips on bumblebee abundance and richness increased with increasing early-season landscape-wide floral resource availability (Figs 2 and S3), stressing the importance of seasonal continuity in resource availability for bumblebees (Williams, Regetz & Kremen 2012; Rundlöf *et al.* 2014). As social species with relatively long colony cycles, bumblebees depend on floral resources from early spring to late summer. Landscapes with higher early-season floral resource availability may attract more nest-searching bumblebee queens in spring (Suzuki *et al.* 2009), and colonies founded in these landscapes generally have a higher production of workers (Westphal, Steffan-Dewenter & Tschardt 2009; Williams, Regetz & Kremen 2012). The larger effects of wildflower strips in landscapes with more early-flowering resources therefore probably result from temporal spillover of the enhanced pool of bumblebees to the late-flowering resources in the wildflower strips (Riedinger *et al.* 2014). Although bumblebee responses to wildflower strip establishment may also be (negatively) affected by land-

scape-wide floral resources during peak flowering of the strips (Carvell *et al.* 2011), variation in bumblebee responses was better explained by landscape-wide floral resource availability prior to peak flowering of the strips (ΔAIC_c of highest ranked model including interaction with late-season landscape-wide resources for bumblebee abundance = 5.49; richness = 4.64).

Landscape structure and land-use intensity, two factors that are known to influence the effectiveness of conservation on farmland (Kleijn *et al.* 2011), did not influence the response of either solitary bees or bumblebees to wildflower strip establishment although the amount of variation in these factors was similar to that in floral resource availability. This highlights the value of using more direct methods to quantify factors that constrain population dynamics of species, such as food or nesting sites, rather than using proxies for limiting factors such as amount of semi-natural habitat or intensity of farming (Hammers *et al.* 2015).

Our results do not provide clear support for bee population responses to the establishment of wildflower strips. Population growth of univoltine bee species depends on the offspring emerging in the year following the year of oviposition, or in the case of bumblebees on the number of colonies founded in the year following the year of queen production. Consequently, a positive effect of wildflower strips on population sizes can only become apparent in the second year after establishment of the strips. The BACI approach used in this study accounts for differences in baseline conditions, but does not correct for variation in floral resource availability between years. This makes it difficult to state with certainty whether, for example, in the UK the increased number of bumblebees from 2012 to 2013 is the result of increased worker production, increased population size or of a foraging response to the steadily increasing floral resources in the UK strips (Figs 1g and S1g,h). In the other countries, the effect sizes of bee responses were similar in the 2 years after wildflower strip establishment. This suggests that in 2012 the experimentally enhanced bee forage resources in the wildflower strips were insufficient to noticeably enhance their reproductive output and therefore bee numbers in 2013. We cannot altogether rule out population-level effects, as enhanced bee densities may have diluted in the surroundings of the strips in the second year after establishment. Nevertheless, in both years, the observed positive effects of wildflower strips most likely reflect spatio-temporal behavioural responses. This may indicate that size of the strips (300 m²) was too small and/or the 2-year monitoring period after establishment of the strips too short to detect clear population responses. Alternatively, bee populations could have been limited by other factors, notably nesting sites (Steffan-Dewenter & Schiele 2008).

SYNTHESIS AND APPLICATIONS

Our study shows that the extent to which establishment of wildflower strips enhanced local flower richness was

one of the main factors determining the effectiveness of the strips, regardless of landscape compositional differences between countries. It suggests that effectiveness of wildflower strips can be enhanced by increasing the number of flowering plant species in seed mixtures. Furthermore, management targeted at maintaining high flower richness in the years after establishment of wildflower strips is pivotal to sustaining positive effects of this conservation measure.

How and where these measures can best be implemented depends on the conservation objectives. If the objective is to promote pollination services, which are mainly supplied by common, generalist species, wildflower strips are expected to be most effective in intensively farmed, resource-poor landscapes dominated by arable fields (Kleijn *et al.* 2011). Besides establishing and maintaining flower-rich wildflower strips, the positive relationship between flower richness and bee densities in control field boundaries suggests that a lot can be gained if management of existing non-cultivated habitats would be adapted to facilitate the development of more flower-rich vegetation (Noordijk *et al.* 2009). Such management regimes would also benefit the seasonal continuity of floral resource availability required by species with long colony cycles such as bumblebees. In contrast, if the main objective is to promote endangered bee species, wildflower strips should include the specific preferred host plants of the targeted declining bee species (e.g. Fabaceae, Lamiaceae, Caprifoliaceae, Campanulaceae; Scheper *et al.* 2014) and should preferably be implemented in landscapes that already host-rich bee communities (Pywell *et al.* 2012).

Our study shows that for mobile invertebrate species, population-level effects of conservation management are difficult to infer, even from multiyear, well-replicated studies that include baseline information. Further research, incorporating the measurement of population dynamical variables, is needed to establish whether and under what circumstances establishment of wildflower strips promotes bee population growth.

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Data accessibility

Data available from the Dryad Digital Repository: doi:10.5061/dryad.f8vs9 (Scheper *et al.* 2015).

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Supporting Information

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

Appendix S1. Methods for quantification of landscape-wide floral resource availability.

Appendix S2. References for conservation status of bee species.

Fig. S1. Mean flower cover and species richness in flower strips and control field boundaries.

Fig. S2. Mean species richness of bumblebees and solitary bees in flower strips and control field boundaries.

Fig. S3. Conditional partial regression plots for the best model explaining the relative change in bumblebee richness between 2011 and 2013.

Table S1. Nitrogen input, proportion of semi-natural habitat and early- and late-season floral resource availability in landscapes surrounding (1-km radius) wildflower strips and control field boundaries.

Table S2. Model selection results for the effects of environmental factors on the effectiveness of wildflower strips, based on the full data set, including the six deviating UK study sites.

Table S3. Results of contrasts for significant interaction effect of treatment and year on flower cover and richness, bumblebee abundance and richness, and solitary bee abundance and richness.

Table S4. Results of generalized linear models comparing the abundance and species richness of Red Listed bee species in flower strips and control sites.