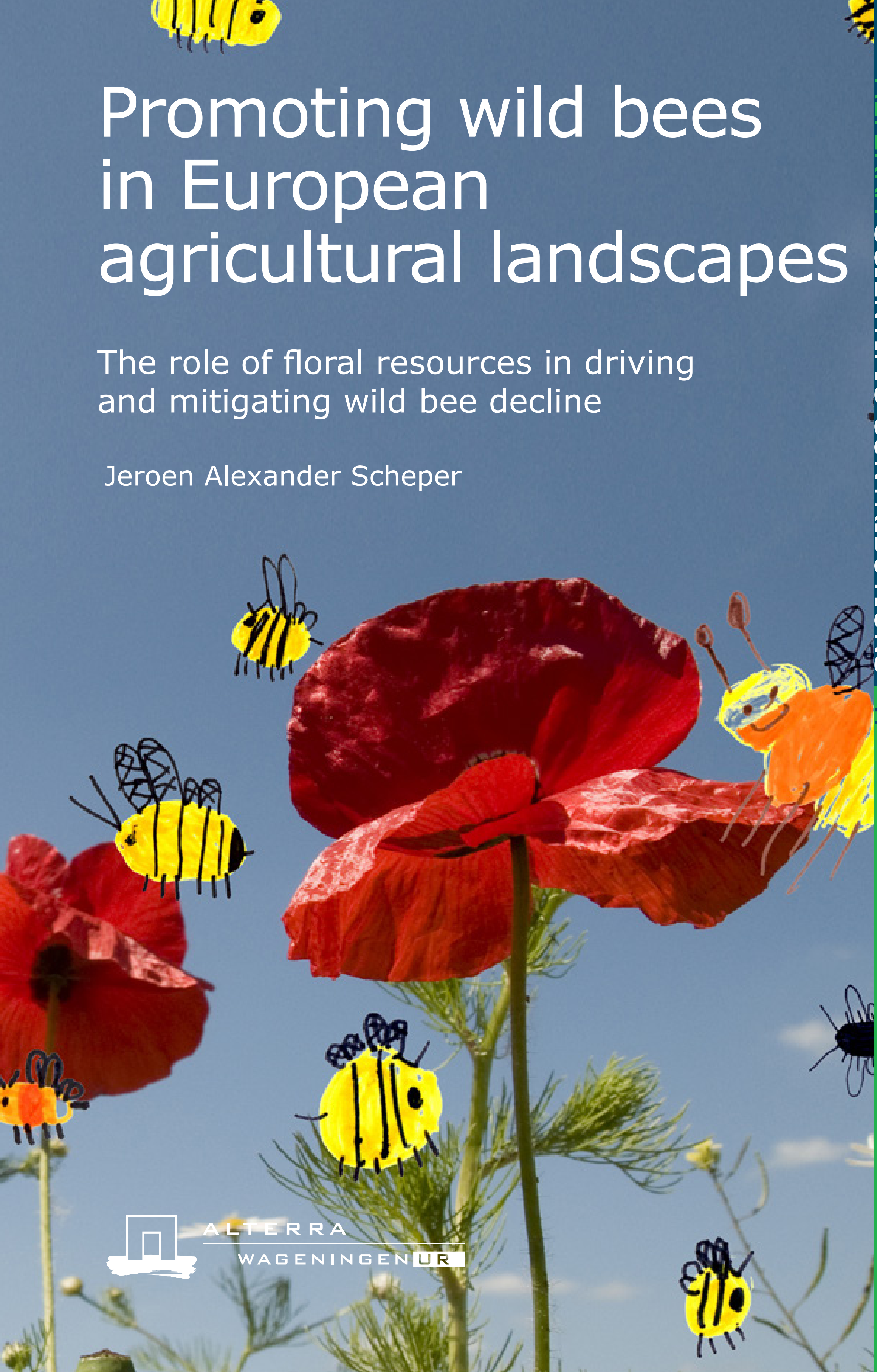
Promoting wild bees in European agricultural landscapes

The role of floral resources in driving and mitigating wild bee decline

Jeroen Alexander Scheper



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Promotoren:
prof. dr. H. Siepel
prof. dr. J.H.J. Schaminée

Copromotor:
prof. dr. ir. D. Kleijn (WUR)

Manuscriptcommissie:
prof. dr. J.C.J.M. de Kroon
prof. dr. G.R. de Snoo (UL)
prof. dr. M.F. Wallis de Vries (WUR)

Contents

CHAPTER 1

General introduction

Wild bees and ecosystem service delivery

Bees (Hymenoptera: Apoidea: Apiformes) comprise a large group of flower-visiting insects, with ca. 20,000 species occurring worldwide (Michener 2007**)** and ca. 2,000 species occurring in Europe (Nieto *et al.* 2014). Flower-visiting insects such as wild bees play a vital functional role in the pollination of both wild plants and crops. The large majority of wild plants are pollinated by insects (Ollerton *et al.* 2011) and insect pollinators thereby form an essential component in the maintenance of biodiverse plant communities and ecosystem functioning. Furthermore, about 75% of the main global food crop species rely on insect-mediated pollination (Klein *et al.* 2007). Although comprising only 35% of global food production volume (Klein *et al.* 2007), insect-pollinated crops provide the majority of many essential vitamins and micronutrients in human nutrition (Eilers *et al.* 2011). The extent to which these crops depend on pollination by insects varies from essential in dioecious (e.g. most kiwi varieties) or self-infertile monoecious crops (e.g. most apple varieties), to beneficial in self-fertile hermaphroditic crops (e.g. strawberry), with insect-pollination enhancing fruit set, seed set, fruit quality and commercial value (Bommarco *et al.* 2012b; Garibaldi *et al.* 2013; Garratt *et al.* 2014; Klatt *et al.* 2014). The area of insect-pollinated crops has increased over the last decades, both at a global and a European scale (Aizen *et al.* 2008; Breeze *et al.* 2014). In Europe, 84% of crop species grown for human consumption, livestock consumption, green manure or essential oils are pollinated by insects (Williams 1994), currently representing 12% of the total EU cropland area (Schulp *et al.* 2014). With the annual economic value of pollination (i.e. the part of the crop yield that can be attributed to pollination) of European food crops estimated at €22 billion (Gallai *et al.* 2009), pollination by flower-visiting insects is a pre-eminent ecosystem service that is of particular economic importance in agricultural landscapes.

A wide variety of insects, such as flies, beetles, wasps and butterflies, may contribute to the pollination of wild plants and crops, but bees generally provide by far the largest contribution (Herrera 1987; Albrecht *et al.* 2007; Jauker *et al.* 2012; Garibaldi *et al.* 2013; King *et al.* 2013). Bees fully depend on floral resources such as pollen and nectar for food provisioning in both their larval and adult life stages. Because of their dependence on floral resources, their foraging behaviour and their morphological adaptations to efficiently collect and transport pollen, bees are considered superior pollinators compared to other flower-visiting insects (Free 1993). The managed honeybee (*Apis mellifera*) has long been regarded as the most important crop pollinator (Klein *et al.* 2007). Managed honeybee colonies provide large numbers of worker bees and can easily be moved to flowering crops to provide abundant pollinators. However, the role of wild bee species has thus far been underestimated (Breeze *et al.* 2011). Recent evidence shows that for most crops wild pollinators are more effective pollinators than honeybees and provide the majority of pollination services, suggesting that honeybees can supplement, but not replace the pollination services of wild pollinators (Garibaldi *et al.* 2013). Even for crops predominantly dependent on honeybees, wild pollinators can play an important indirect role by enhancing the pollination efficiency of honeybees through synergetic effects (Greenleaf & Kremen 2006; Brittain *et al.* 2013). In view of increasing concern about declining numbers of honey bee colonies driven by colony losses and declining number of beekeepers (Potts *et al.* 2010b; Van der Zee *et al.* 2012), wild bees are expected to become increasingly important for pollination of crops in Europe (Breeze *et al.* 2014). Diverse wild bee communities improve the temporal stability of pollination service delivery and can provide insurance of pollination services under environmental change (Garibaldi *et al.* 2011; Bartomeus *et al.* 2013).

However, while pollination service supply of honeybees depends on beekeepers (Potts *et al.* 2010b), pollination by wild bees depends on the availability of foraging and nesting sites in the landscapes surrounding the crops (Schulp *et al.* 2014). Insect-pollinated crops can be attractive and highly rewarding sources of pollen and nectar for wild bees in agricultural landscapes (Westphal *et al.* 2003; Holzschuh *et al.* 2013). However, these crops flower for only a short period of time and the crop monocultures provide an unbalanced food supply for bees (Holzschuh *et al.* 2013; Eckhardt *et al.* 2014). Furthermore, frequent disturbance by agricultural practices (e.g. tillage, pesticide application) generally makes crops unsuitable permanent habitats for bees, especially if intensively managed (Holzschuh *et al.* 2007). To persist in agricultural landscapes, wild bees therefore depend on semi-natural habitats such as forest edges and semi-natural grasslands that provide a more diverse and continuous supply of floral resources and nesting, mating and overwintering sites. Such semi-natural habitats support abundant and diverse bee communities and can act as source habitats for wild pollinators in the agricultural matrix (Tscharntke *et al.* 2005; Öckinger & Smith 2007; Kohler *et al.* 2008). Consequently, pollinator richness and abundance in insect-pollinated crops is higher in landscapes containing more high-quality semi-natural habitats (Kennedy *et al.* 2013; Shackelford *et al.* 2013), and visitation rates, stability of pollination services and crop yields increase with decreasing distance to semi-natural source habitats (Ricketts *et al.* 2008; Garibaldi *et al.* 2011).

Bee declines in agricultural landscapes

While the importance of wild bees as ecosystem service providers is increasingly becoming acknowledged, evidence is mounting that many wild bee species have declined in Europe over the last decades (Biesmeijer *et al.* 2006; Kosior *et al.* 2007; Patiny *et al.* 2009; IUCN 2014). The bee communities of contemporary intensively farmed landscapes have been strongly impoverished (Kleijn *et al.* 2001; Bommarco *et al.* 2012a; Dupont *et al.* 2011). Many previously widespread bee species in agricultural landscapes are now only found in nature reserves (Kohler *et al.* 2008) or (sub)urban refugia (Samnegard *et al.* 2011). It appears that in northwest Europe the rate of decline of wild bee richness has slowed down in recent years (Carvalheiro *et al.* 2013). However, as bee communities have become more homogenized during earlier periods of decline (Carvalheiro *et al.* 2013), the reduced rate of species richness decline probably reflects that bee communities are currently dominated by a limited number of more resilient bee species that remained common.

Climate change, invasive species and spread of pathogens have been identified as potential factors associated with pollinator declines, but land use change and agricultural intensification are generally considered the most important drivers of pollinator loss (Potts *et al.* 2010a; Winfree *et al.* 2011; González-Varo *et al.* 2013). Since the second half of the 20th century, land use change and agricultural intensification have resulted in the loss and fragmentation of habitat, accompanied by increased use of pesticides and fertilizers (Stoate *et al.* 2001; Benton *et al.* 2003; Tscharntke *et al.* 2005). A recent quantitative review investigating the effects of different types of disturbances on bee communities identified habitat loss and fragmentation as the most import negative disturbances for bees (Winfree *et al.*, 2009). Both habitat loss and increased pesticide use negatively affect pollinators through repercussions on the direct factors (sensu Roulston & Goodell 2011) that regulate pollinator populations, such as the availability of food resources, the availability of nesting, mating and overwintering sites, and incidental risk factors (i.e. biotic and abiotic sources of mortality). Loss of floral resources is generally thought to be the main driver for bee decline in contemporary anthropogenic landscapes (Carvell *et al.* 2006; Winfree *et al.* 2011), but so far this remains speculative.

Mitigation measures for bee loss

Besides their adverse effects on intrinsic values of bee biodiversity, the negative effects of land use change and agricultural intensification on wild bees have potentially detrimental effects on the delivery of pollination services, causing pollination deficits in wild plants and insect-pollinated crops (Potts *et al.* 2010a; Garibaldi *et al.* 2013). This is strikingly exemplified by the contrasting yield trends for pollinator-dependent and pollinator-independent crops over the last decades. Agricultural intensification has increased yields of pollinator-independent, but not of pollinator-dependent crops, and has decreased the stability of the yields of pollinator-dependent crops (Deguines *et al.* 2014). Consequently, reported bee declines have raised concerns about loss of both pollination services and intrinsic biodiversity values, and have increased the need for effective measures to mitigate pollinator loss. In general, halting and reversing the adverse effects of land use change on bee communities may be achieved by a combination of the conservation of remaining semi-natural habitats, thereby preventing further loss of bee habitats, and the creation or restoration of bee habitat. Nature reserves protect remaining (semi-)natural areas from conversion to cropland, pasture, plantation forest or urban areas, and as such are key components for the conservation of bee biodiversity (Westrich 1996; Kohler *et al.* 2008). However, with farmland covering about 47% of the land area in Europe (EC 2010), conservation measures on farmland are essential to support bee communities in intensive agricultural landscapes.

In Europe, there has been much research on how to mitigate pollinator loss on farmland through voluntary conservation measures such as agri-environment schemes (e.g. Kleijn *et al.* 2006; Carvell *et al.* 2007; Holzschuh *et al.* 2007; Potts *et al.* 2009). Since the early 1990s various agri-environment schemes have been implemented to counteract the adverse effects of modern agriculture on biodiversity. These schemes provide farmers financial incentives to restrict farming intensity or to create or maintain non-cropped farmland habitat such as field margins, hedges and wildflower strips. Although the effectiveness of agri-environment schemes at conserving biodiversity in general has been questioned (Kleijn & Sutherland 2003), several of these may potentially be beneficial to bees and other pollinators. Yet, agri-environment schemes are, with the exception of some UK and Swiss schemes, not specifically targeted at pollinators (Haaland *et al.* 2011) and evaluations of the effectiveness of agri-environment schemes in promoting pollinators have shown mixed results (Kleijn *et al.* 2006). Whether and to what extent agri-environmental measures benefit pollinator communities has been suggested to depend on the type of measures and where they are implemented (Kleijn *et al.*, 2006; Kohler *et al.*, 2007), what genus or order of pollinators is being targeted (Kohler *et al.*, 2007) and the composition of the landscape in which the measures are implemented (Holzschuh *et al.*, 2007; Rundlöf *et al.*, 2008). However, although agri-environment schemes have been part of European conservation policies for more than twenty years, it is still poorly understood what mechanisms drive the effectiveness of these schemes in promoting pollinator biodiversity.

Aims and outline of the thesis

The main objective of this thesis is to evaluate and understand the effectiveness of mitigation measures for loss of wild pollinators in European agricultural landscapes. To develop effective mitigation strategies it is essential to identify and address the main causes underlying pollinator decline. Furthermore, in view of the controversy surrounding the effectiveness of conservation measures on farmland, it is pivotal to know what ecological factors explain success or failure of these measures. Focussing primarily on bees, the most important pollinators of wild plants and crops, this thesis therefore investigates what species traits and ecological mechanisms affect the effectiveness of mitigation measures, thereby providing insight in what measures are effective where and for what pollinator taxa. We specifically focus on the role of floral resources in driving bee decline and asses the importance of floral resources in determining the effectiveness of mitigation measures for decline.

Using a trait-based approach and an extensive database on historical bee species distributions, Chapter 2 examines the relative importance of a range of proposed factors responsible for wild bee decline and specifically tests whether bee decline is caused by loss of floral resources. Chapter 3 reviews what is known about the impact of conservation measures on farmland, and provides a theoretic framework for the ecological processes and mechanisms affecting the effectiveness of these measures in conserving farmland biodiversity. In Chapter 4 the validity of this framework is tested for bees, hoverflies and butterflies. Using a meta-analytic approach, this study examines what environmental factors affect the effectiveness of European agri-environment schemes in promoting pollinators in agricultural landscapes. Chapter 5 presents the results of a field experiment, carried out in four European countries, that evaluates the effectiveness of an agri-environmental measure specifically targeted at wild bees. More specifically, this experiment investigates whether variation in effects of wildflower strips across countries can be explained by the interplay of local and landscape-wide floral resource availability, and tests whether the observed foraging responses are indicative of actual population increases or merely reflect spatiotemporal aggregation responses. Chapter 6 provides a more in-depth analysis of the potential population-level effects of these wildflower strips. In this experiment, artificial trap nests are used to measure reproductive responses of cavity-nesting bee species to implementation of wildflower strips. Finally, the general discussion in Chapter 7 integrates the findings reported in the different chapters in this thesis. The results are put in a wider context, their implications for conservation management in agricultural landscapes are discussed, and future directions for further research are suggested.

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CHAPTER 2

Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands

Jeroen Scheper[1], Menno Reemer[2], Ruud van Kats[1], Wim A. Ozinga[3,4], Giel T.J. van der Linden[5], Joop H.J. Schaminée[3,4], Henk Siepel[6,7] & David Kleijn[1,5]

[1]Alterra, Animal Ecology Team, 6700 AA Wageningen, The Netherlands; [2]Naturalis Biodiversity Center, European Invertebrate Survey - the Netherlands, 2300 RA Leiden, The Netherlands; [3]Radboud University Nijmegen, Institute for Water and Wetland Research, Experimental Plant Ecology, 6500 GL Nijmegen, The Netherlands; [4]Alterra, Team Vegetation, Forest and Landscape Ecology, 6700 AA Wageningen, The Netherlands; [5]Wageningen University, Resource Ecology Group, 6700 AA Wageningen, The Netherlands; [6]Wageningen University, Nature Conservation and Plant Ecology Group, 6700 AA Wageningen, The Netherlands; [7]Radboud University Nijmegen, Institute for Water and Wetland Research, Animal Ecology & Ecophysiology, 6500 GL Nijmegen, The Netherlands.

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Abstract

Evidence for declining populations of both wild and managed bees has raised concern about a potential global pollination crisis. Strategies to mitigate bee loss generally aim to enhance floral resources. Yet, we do not really know whether loss of preferred floral resources is the key driver of bee decline because accurate assessment of host plant preferences is difficult, particularly for species that have become rare. Here we examine whether population trends of wild bees in the Netherlands can be explained by trends in host plants and how this relates to other factors such as climate change. We determined host plant preference of bee species using pollen loads on specimens in entomological collections that were collected before the onset of their decline, and used atlas data to quantify population trends of bee species and their host plants. We show that decline of preferred host plant species was one of two main factors associated with bee decline. Bee body size, the other main factor, was negatively related to population trend which, because larger bee species have larger pollen requirements than smaller species, may also point towards food limitation as a key factor driving wild bee loss. Diet breadth and other potential factors such as length of flight period or climate change sensitivity were not important in explaining 20th century bee population trends. These results highlight the species-specific nature of wild bee decline and indicate that mitigation strategies will only be effective if they target the specific host plants of declining species.

Significance Statement

Growing concern about bee declines and associated loss of pollination services has increased the urgency to identify the underlying causes. So far, the identification of the key drivers of decline of bee populations has largely been based on speculation. We assessed the relative importance of a range of proposed factors responsible for wild bee decline and show that loss of preferred host plant species is one of the main factors associated with the decline of bee populations in the Netherlands. Interestingly, species foraging on crop plant families have stable or increasing populations. These results indicate that mitigation strategies for loss of wild bees will only be effective if they target the specific host plants of declining bee species.

INTRODUCTION

Pollinating insects such as bees play an essential role in the pollination of wild plants (1) and crops (2). However, reported population declines in both wild and managed bees (3-5) have raised concerns about loss of pollination services and triggered interest in identifying the underlying causes for bee decline (6). Land use change and agricultural intensification are major drivers of biodiversity loss in general (7, 8) and are considered the most important environmental drivers of loss of wild bee diversity in particular (6, 9). It is generally believed that these drivers affect bees, which depend on floral resources in both their larval and adult life stages, through repercussions on the availability of floral resources in contemporary anthropogenic landscapes (9, 10, 11), but so far scientific evidence that loss of floral resources is driving bee decline is lacking. Nevertheless, current strategies to mitigate bee decline focus primarily on enhancing floral resources (12). To prioritize and develop effective mitigation strategies it is essential to identify the mechanisms underlying bee population trends and assess whether these are mediated by floral resources.

Although bees as a group are declining, individual species show more variable responses, with some species declining sharply while others remain stable or even increase under current land use change and agricultural intensification (3, 4, 13). These differential responses can be used to disentangle the effects of floral resource availability from those of other potential factors affecting bee population trends. The proportion of the floral resources in contemporary anthropogenic landscapes that can be used for forage by a bee species depends on its diet breath and host plant preference, and it may be expected that species that have declined have a narrower diet breadth and prefer host plants that have declined (14, 15). However, diet breadth and host plant preference of bee species is difficult to assess. Presently observed host plant use does not necessarily reflect actual preference, as preferred host plants may have gone locally extinct and bees that have declined may have become restricted in their food choice in their remaining habitats (15). In addition, if host plant use is measured for more individuals of abundant, widespread species than for rare ones, an apparent link between diet breadth and population trend may simply arise as a sampling artefact (16). Furthermore, the relationship between host plant use and population trend may be confounded by species' rarity prior the onset of major environmental changes (17), as rarity in itself increases susceptibility to stochastic events (18) and has been shown to be one of the most important factors predicting population decline in various taxa (19-21). Surprisingly, to our knowledge none of the studies that have so far examined the relationship between diet breadth and/or host plant preference and bee population trends have taken species' initial rarity into account (e.g. 3, 4, 15, 22). Other factors, such as body size (4, 23), phenology (4, 22) and sensitivity to climate change (4, 24, 25) may be associated with bee decline as well, and to date the relative importance of diet breadth and pollen host plant preference in explaining bee population trends remains unclear.

Here we solve this problem by analysing historical pollen preferences of wild bees (15). Bees are generally more selective in their choice of food plants when foraging for pollen (source of protein and minerals for both larvae and adults) than nectar (source of energy) (26, 27). Distributional changes in plant species from which pollen are collected therefore probably exerts a larger influence on bee populations than changes in nectar plants. We investigate whether and to what extent loss of preferred floral resources drives bee population trends in the Netherlands, one of the most human-modified and intensively farmed countries in the world. Over the course of the 20th century, agriculture has intensified in the Netherlands (Fig. S1) and the area of semi-natural habitat preferred by bees has diminished to only one fifth of the area at the beginning of the 20th century (Fig. S2). More than half of the bee species are currently on the national Red List (28). As such this country is a particularly suitable study area to identify critical factors associated with bee population decline.

We assessed pollen host plant use of bee species independently from their population trends by analysing pollen loads on the bodies of bee specimens that were collected before 1950 (15), prior to the onset of agricultural intensification in the Netherlands. Altogether our analysis included trend and trait data of 57 bee species in ten genera and four subfamilies (Table S1). We calculated population trend indices for bee species and their host plants (period 1902-1949 vs. 1975-1999) using extensive national species distribution datasets (13, 29). Linear mixed models, with bee subfamily as a random factor to account for phylogeny, and a multi-model inference approach was used to examine the relationship between bee population trends and pollen host plant use, simultaneously taking into account differences in species' rarity prior to the onset of agricultural intensification and other factors that have been proposed to explain bee population trends.

RESULTS AND DISCUSSION

Model averaging across our set of candidate models (Δ AIC$_c$ < 4) (30) revealed that population change of pollen host plants (full-model averaged standardized regression coefficient $\beta = 0.54$; relative variable importance $\omega_p = 1.00$), body size ($\beta = -0.60$; $\omega_p = 1.00$), and range size before 1950 ($\beta = 0.20$; $\omega_p = 0.72$) were the most important factors associated with bee population trends (Table 1). A model with just these three predictors best explained wild bee population change between the periods 1902-1949 and 1975-1999. It suggests that bee population trends were positively related with host plant change index (Fig. 1a) and initial range size (Fig. 1c) and negatively related with body size (Fig. 1b). This model explained 50% of the variation in bee population responses and had a probability of 0.37 of being the best model among the seven models in the candidate set. Analysis of bee trends based on a more extensive dataset that also included more recent bee records (period 1900-1989 vs 1990-2011 (13)) produced similar results (Table S2).

Table 1. Model selection and model averaging results for candidate models explaining bee population trends

	Model									
Predictor	1	2	3	4	5	6	7	β	95% CI	ω_p
Change of host plants	0.54	0.53	0.55	0.53	0.53	0.54	0.58	0.54	**0.29 to 0.79**	1.00
Body size	-0.63	-0.62	-0.51	-0.51	-0.64	-0.63	-0.49	-0.60	**-0.89 to -0.31**	1.00
Range size before 1950	0.29	0.25			0.30	0.28		0.20	-0.14 to 0.54	0.72
Diet breadth		0.11		0.18				0.03	-0.14 to 0.21	0.25
Length of flight period					-0.02		0.11	0.00	-0.11 to 0.12	0.15
Phenological advancement						0.01		0.00	-0.07 to 0.08	0.10
Δ AIC$_c$	0.00	1.89	2.21	2.56	2.58	2.60	3.93			
ω_m	0.37	0.14	0.12	0.10	0.10	0.10	0.05			

Candidate models are ranked in order of increasing differences in corrected Akaike information criterion (Δ AIC$_c$). Explanatory variables were standardized by centering and dividing by 2 standard deviations. Akaike model weights (ω_m) indicate the probability that a model is the best approximating model given the set of models considered. For each predictor the parameter estimate for each candidate model is given, along with its model averaged estimate (β) (including zeros for variables that are not in a particular model), 95% confidence interval, and relative importance (ω_p). Confidence intervals not overlapping zero are indicated in bold.

Our data does not enable us to distinguish whether the observed link between population trends of bees and their preferred host plants results from plant declines causing bee declines or vice versa. However, circumstantial evidence argues in favour of the proposition that it is primarily the loss of preferred host plants that is causing bee decline. First, distribution changes of plants in the Netherlands do not differ among insect-pollinated, wind- or water-pollinated, and self-pollinating plants (3), which reflects that loss of plant diversity in the Netherlands is mainly driven by abiotic factors associated with land use change, such as eutrophication, desiccation and acidification (31, 32). Second, most insect-pollinated plants are pollinated by a diverse array of both generalist and specialist pollinators (33), which makes them fairly robust to the loss of a subset of pollinators. Bee losses may for instance have been compensated for by the increase of others important groups of pollinators such as hoverflies. Hoverflies, whose larvae do not depend on floral resources, have not been negatively affected by land use change and have even increased in the Netherlands over the last decades (3). Finally, a recent study on plant-pollinator networks in grasslands shows that land use intensity primarily drives loss of host plants, and that loss of host plants subsequently drives bee decline while the reciprocal effects are not pronounced (34).

Length of flight period (β = 0.004; ω_p = 0.15) and the degree of phenological advancement of the flight periods of bees between 1902-1949 and 1975-1999 (climate change sensitivity) (β = 0.001; ω_p = 0.10) hardly explained bee population trends (Table 1). Mean daily temperatures during the activity period of bees (April – September) have increased in the Netherlands between 1906 and 2012 (Fig. S3). Yet, the extent to which bees advanced their flight periods in response to these rising temperatures did not contribute to explaining differences in bee population trends. This may indicate that bee species did not suffer from phenological mismatches with their host plants (35).

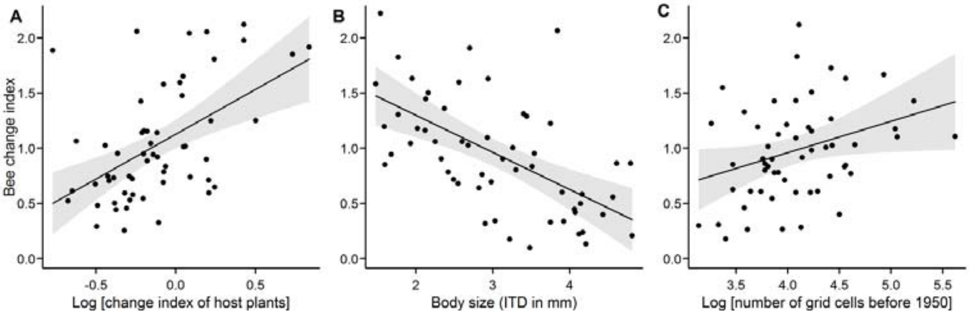

Figure 1. Relationship between bee population trends and body size, change index of pollen host plants and initial rarity of bee species. Partial regression plots based on the best model in the candidate set for (*A*) log-transformed weighted mean change index of pollen host plants in bee species' pollen diets, (*B*) body size measured as the inter-tegular distance (ITD) and (*C*) log-transformed number of occupied 5 × 5 km grid cells before 1950. Note that a bee change index of 1 indicates no change. Plotted points represent partial residuals. Shaded areas indicate 95% confidence bands.

Surprisingly, diet breadth, i.e. the number of different pollen host plants used by a bee species, was also only of minor importance in explaining bee population trends ($\beta = 0.03$; $\omega_p = 0.25$, Table 1). Species that use only a narrow array of food resources are generally expected to be more vulnerable to decline under environmental change (36). However, our results indicate that bee species that use a low number of host plant species are not necessarily susceptible to decline, as long as their preferred host plants are not declining. Likewise, the more generalist species may be expected to decline if their most important host plants decline. Even the most generalist bee species are restricted in their range of host plants and have distinct preferences for certain pollen taxa (37). Bees may produce lower quality offspring when larvae are reared on pollen of less preferred host plants (38) or may fail to produce offspring altogether (39). Declining bee species therefore most likely suffered from reduced fitness as a consequence of the loss of their preferred host plant species.

The extent to which bee species' preferred host plants declined appeared to be associated with phenology. The population change of pollen host plants was negatively correlated with the timing of the beginning of the flight period of bee species ($r = -0.53$, $P < 0.001$; Fig. 2a), suggesting that particularly the late-flowering host plants have declined over the past century. In addition, an inventory of landscape-wide floral resource availability in sixteen Dutch agricultural landscapes in 2012 showed that late-season floral resource availability is significantly lower than early-season resource availability (paired t-test, $t_{15} = 8.30$, $P < 0.001$; Fig. 2b). In contemporary intensively used agricultural landscapes, mass-flowering crops (e.g. *Brassica napus*), flowering trees and shrubs (e.g. *Salix* spp., *Prunus* spp.), and flowering herbs in improved grasslands and field margins (e.g. *Taraxacum* spp., *Cardamine pratensis, Ranunculus* spp.) still provide ample early-season floral resources. However, later in the season the availability of floral resources is strongly reduced because shrubs and trees have ceased flowering, grasslands have been grazed or cut for silage and field margins have been mown. Taken together, these results suggest that floral resources are particularly limiting for bees that emerge later in the season.

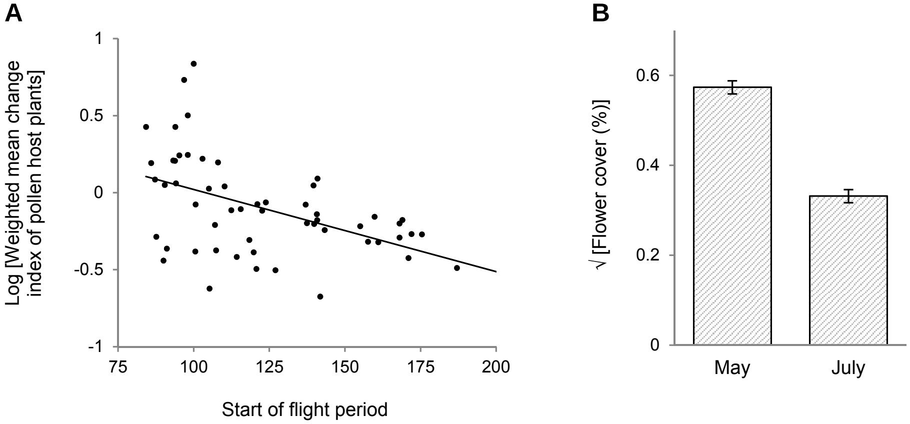

Figure 2. Seasonal pattern of pollen host plant change and floral resource availability. (*A*) Relationship between the beginning of the flight period of bee species (number of days after 31 December) and the log-transformed weighted mean change index of pollen host plants in their pollen diets. (*B*) Mean estimated spring and summer floral resource availability (square root transformed flower cover) in 16 agricultural landscapes (1 km radius) in the Netherlands in 2012. Error bars represent s.e.m. adjusted for paired observations.

The observed negative relationship between bee body size and population trend may result from the decline of the large-bodied bumblebee species, which as a group have experienced particular strong declines in Europe (13, 40). However, body size remained a key factor (β = -0.39; ωp = 0.93) even when the ten bumblebee species were excluded from the analysis, suggesting that the negative relationship with body size does not only reflect the decline of the bumblebees. Alternatively, the effect of body size may be linked to loss of floral resources as driving factor for wild bee decline. Large bee species may be more susceptible to land use change than smaller ones (4, 23) because of their larger pollen quantity requirements (41). In homogenous, intensively farmed landscapes, declining floral resources may cause fewer problems for small species to find sufficient food for offspring production than for large species, despite their larger foraging range (42).

To identify whether bee decline was associated with preference for specific plant families, we calculated for each plant family the mean trend index of bees that relied for at least 10% of their pollen diet on that particular plant family (Fig. 3). On average, bee species that preferentially collected pollen from plant species belonging to the Rosaceae family significantly increased while bees feeding on plants in the Fabaceae family decreased. This pattern remained when threshold values of 20% or 30% were used (Fig. S4). The declines in Fabaceae species can be attributed to the loss of Fabaceae-rich semi-natural grasslands (14), but also to the drastic decrease of the agricultural use of Fabaceae as (fodder) crops during the 20th century (Fig. S5). Our findings shed new light on the consequences of reported losses of wild bees for crop pollination. Bees that preferentially collect pollen from Rosaceae, Brassicaceae and Asteraceae species, which contain major insect-pollinated crops such as apple, strawberry, oil-seed rape and sunflower, have remained stable or actually increased. Delivery of crop pollination services by wild bees may therefore be under less threat from land use change pressures than conservation of wild bee diversity.

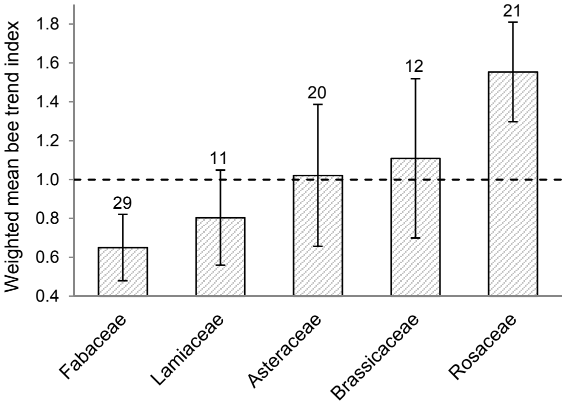

Figure 3. Weighted mean population trends of bee species visiting the most frequently used host plant families. Mean population trends, weighted by the percentage pollen contribution of the host plant families to bee species' diets, are based on bee species that relied for at least 10% of their pollen diet on a particular plant family. Results are shown for plant families that made up at least 10% of the pollen diets of at least ten bee species. Error bars indicate weighted 95% confidence intervals. Numbers above bars indicate sample size.

Because it is impossible to experimentally examine causes of large scale population declines, it is difficult to establish causal relationships between drivers and population trends. The robust linkage of bee population trends, through historical host plant preferences, to plant population trends that was found in this study therefore probably represents the best possible evidence for key factors causing bee population decline in intensively farmed landscapes for some time to come. These insights will help us develop more effective ways to mitigate loss of species that are threatened in their existence as well as promote bees important for delivery of crop pollination services.

METHODS

Examined bee species. In the Netherlands 357 wild bee species are found. A total of 256 species actively collect and transport pollen to provision their offspring. The remaining bees are cleptoparasitic bees that lay their eggs in brood cells of host bees and do not forage for pollen themselves. We focused our sampling efforts on bee species that use multiple host-plant species ('polylectic bee species'), which constitute 70% of the pollen-collecting bee species in the Netherlands (13). We used the number of 5 × 5 km grid cells occupied before 1950, obtained from the national bee distribution database (13), to assess species' rarity before the onset of major environmental change, and only included species if they were common (present in at least 150 5 × 5 km grid cells), fairly common (70 – 149 grid cells) or only moderately rare (20 - 69 grid cells) before 1950. Bee species from the genus *Hylaeus* were excluded because female bees of these species transport pollen internally in their crops rather than externally on their bodies, which makes non-destructive sampling of pollen difficult. This resulted in a total of 75 bee species for which we aimed to determine pollen host plant use (see below).

Bee population trends. Relative bee population trends were determined using the national bee distribution database of European Invertebrate Survey (EIS) - the Netherlands (13). This database contains 186,147 records of bees collected and observed in the Netherlands between 1809 and 2011. Relative change indices for the focal bee species were calculated as the ratio between the number of occupied 5 × 5 km grid cells in the period 1902-1949 (26,749 records) and the number of occupied grid cells in the period 1975-1999 (45,447 records), divided by the average of the change ratio of all focal bee species. Relative change indices thus reflect bee species' performance between the two periods relative to the average performance of all the species considered. We only used data of grid cells that were inventoried in both periods (total of 568 cells) and, to avoid potential bias arising from the much larger proportions of field observations in the database in recent years (which are mainly restricted to common and easily recognizable species), only included records from natural history collections. Sampling intensity differed between periods, which, as the probability that a species is recorded depends on sampling intensity, may introduce bias when comparing grid cells between both periods. Therefore, using the total number of bee records per period as a proxy for sampling intensity, we corrected for differences in sampling intensity between periods by multiplying the number of grid cells each species occupied in 1975-1999 with the quotient of the total number of bee records in 1902-1949 divided by the total number of bee records in the 1975-1999 period (13). The rationale behind comparing the 1902-1949 and 1975-1999 periods is that these periods form the basis for the national red list of vascular plant species (29) (see below) and contrast a period of low intensity farming with a period of intensive agriculture and reduced availability of semi-natural bee habitat (Fig. S1 and Fig. S2). However, to assess whether the results of our study were robust to the chosen time periods, we also analysed the drivers of wild bee decline using bee trends based on the periods used by Reemer *et al.* (13) [1900-1989 (77,920 records) vs. 1990-2011 (68,491 records), total of 858 grid cells]. Using trends based on these time periods produced results similar (Table S2) to the results reported in the main text (Table 1).

Pollen host plant use. Pollen loads of female bees of the selected species were sampled in the entomological collections of the Natural History Museums of Amsterdam, Leiden, Leeuwarden, Rotterdam, Tilburg, Wageningen and Brussels (Belgium). Only specimens were sampled that were collected before 1950 (between 1870 and 1950) and that had pollen in the pollen-carrying bodily structures (scopa or corbicula). Samples of pollen from each pollen load were mounted in glycerine jelly containing basic fuchsin to stain the pollen grains. Identification was done using a light microscope at 400× magnification with the assistance of a reference pollen collection of approximately 130 species and reference documents (43). Pollen grains were identified to the lowest possible taxonomic level, mostly to genus (67%). For each sample, we estimated the percentage contribution of each pollen taxon, with pollen taxa contributing <5% not being considered as they may result from contamination. To avoid potential bias resulting from several samples collected at the same location at the same date, duplicate samples were randomly excluded from the dataset.

We could not reliably determine pollen host plant use for 18 of the selected 75 species because of insufficient numbers of pollen samples ($n < 15$) in museum collections and these species were omitted from further analyses. The mean number of pollen samples per species of the final set of 57 bee species was 28.9 (min = 15, max = 63). These 57 species (Table S1) represent 40% of the pollen collecting bee species that were observed in at least twenty 5 × 5 km grid cells in the Netherlands before 1950. The majority of the specimens of these species were collected at locations in the Netherlands but a limited number (7%) was collected at Belgian locations near the Dutch-Belgian border. Out of the total number of 1,646 specimens, broadly equal numbers of specimens were collected in the southern and northern part of the study area (respectively 863 and 783). In total, we identified 170 different pollen taxa in the pollen loads of the 57 focal bee species.

Following Kleijn & Raemakers (15), we quantified pollen host plant preference for each bee species as the percentage contribution of each pollen taxon to the total pollen load sampled from all specimens of the bee species. Population changes of pollen host plants during the 20th century were based on the frequency of occurrence of plant species in 1 × 1 km grid cells in the periods 1902-1949 (1.7 million records) and 1975-1999 (3.5 million records) (29, 44). We calculated relative change indices of host plants as the ratio between the number of occupied grid cells in the period 1902-1949 and the number of occupied grid cells in the period 1975-1999, divided by the average of the change ratio of all identified bee host plants. Change indices were based on a selection of 7,374 grid cells with multiple observations within the grid cell across both periods (nearly 25% of the land surface of the Netherlands), corrected for temporal differences in sampling intensity (29). For pollen taxa that could only be identified to genus or family level, we used distribution data of the common plant species in the respective genus or family to calculate a weighted average change index for these pollen taxa (15). Next, for each bee species we calculated the weighted mean population change index of the host plants in its pollen diet (CI_{diet}) as

$$CI_{diet} = \frac{\sum_{i=1}^{n} PC_i \times CI_i}{\sum_{i=1}^{n} PC_i}$$

with PC_i representing the percentage contribution of pollen taxon i to the total observed pollen load of the bee species, CI_i the relative change index of pollen taxon i, and n the total number of pollen taxa observed in the pollen loads of the bee species. Pollen diet breadth, i.e. the number of pollen taxa in the pollen diets of bee species, was determined after sample-based rarefaction to fifteen samples using EstimateS software (45).

Other factors associated with bee decline. For each bee species we assessed its initial rarity, body size, phenology and response to climate change. First, as rarity in itself may be an important cause of population decline (18) and may confound any observed relationship between bee traits and population trends (17), we quantified species' rarity before the onset of major land use changes in the Netherlands as the number of 5 x 5 km grid cells before 1950.

Second, we measured bee body size as the inter-tegular distance (ITD). The ITD is the distance between the two insertion points of the wings, which is a reliable estimator of bee body size (46). For all species, except *Bombus* species, we measured the ITD of ten female specimens. For *Bombus* species we measured the ITD of twenty worker bees to account for larger intraspecific variation in body size in these species.

Third, we determined the start and length of the flight periods of bees using the national bee distribution database of European Invertebrate Survey (EIS) - the Netherlands (13). For both the 1902-1949 and 1975-1999 periods, we used the records in the bee database (mean number of records per species 1902-1949 = 92; 1975-1999 = 374) to calculate the 10th and 90th percentile of the recording day (1 January = 1) for each bee species and defined the 10th percentile as the start, and the number of days between the 10th and 90th percentile as the length of the flight period of bee species (4). Seven species had become too rare (less than 40 records) to reliably determine their flight periods in the period 1975-1999. For these species, we predicted the start and length of the flight period using the linear relationships between the other species' start of flight period ($\text{Start}_{1975\text{-}1999} = 0.896 \times \text{Start}_{1902\text{-}1949} + 14.629$, $F_{1,49} = 484.1$, $P < 0.001$, $R^2 = 0.91$) and end of flight period in 1902-1949 and 1975-1999 ($\text{End}_{1975\text{-}1999} = 0.920 \times \text{End}_{1902\text{-}1949} + 15.929$, $F_{1,49} = 421.7$, $P < 0.001$, $R^2 = 0.90$). We quantified the influence of climate change by calculating the phenological advancement of bee species' flight periods between both periods ($\text{Start}_{1975\text{-}1999} - \text{Start}_{1902\text{-}1949}$).

Although nesting ecology may be expected to be an important factor underlying differential responses of bee species to land use change (11, 47), still little is known about the nesting requirements of most bee species and nesting ecology is difficult to quantify. Rough categorical classifications of bee species' nesting ecology (e.g. nesting above-ground vs. nesting below-ground) oversimplify the broad array of nesting habitats, substrates and construction materials used by different bee species (48) and probably obscures any relationship between bee species' nesting ecology and population response to land use change. Possibly as a consequence, previous analyses did not find any relationship between nesting ecology and population trends of species (4). We therefore chose not to include any categorical measure of nesting ecology in our analysis.

Floral resource availability in contemporary agricultural landscapes. In 2012 we used a stratified sampling approach to estimate spring and summer floral resource availability in 16 agricultural landscapes (1 km radius) in the Netherlands. Flower inventories were conducted in habitats in seven main land use classes: semi-natural habitats (e.g. forest edges, wooded banks), cultivated grasslands, non-flowering crop fields (e.g. maize fields, wheat fields), flowering crop fields (oilseed rape fields), uncultivated field boundaries (field boundaries, ditch banks, road verges), non-flowering perennial habitats (forest interiors) and gardens. Flower inventories were performed twice: once in May and once in July. For each of the land use classes we estimated percentage cover of flowering forbs in randomly selected plots (100 m^2), evenly spread out over the study landscapes (grand total of 48 plots). We used GIS to calculate the area of land use classes in the 1-km radius study landscapes, and calculated the estimated total landscape-wide floral resource availability (% cover) in May and July in each landscape as: (mean flower cover land use class A × proportion of land use class A in the study landscape + mean flower cover land use class B × proportion of land use class B in the study landscape + ….) / 100.

Data analysis. We used linear mixed models and an information-theoretic approach to assess to what extent the explanatory variables were related to bee population trends. We constructed a set of linear mixed models containing all possible combinations of the different predictors, including an intercept only model. As phylogenetic analyses are controversial (49) and phylogenetic trees for bees are continuously challenged (50), we did not use phylogenetic regression, but instead included bee subfamily as a random factor to account for potential non-independence of trends and traits among closely related bee species (4). The variables "range size before 1950" and "change of host plants" were log-transformed to reduce positive skew. We excluded start of flight period (correlated with change of host plants, $r = -0.53$, $P < 0.001$) from the set of predictors to avoid multicollinearity. A multi-model inference approach that used start of the flight period instead of change in host plants showed that the highest ranking model that included start of flight period ($AIC_c = 90.3$, Akaike model weight $\omega_m = 0.016$) was 62 times less likely to be the best model than the highest ranking model that included change in host plants ($AIC_c = 82.0$, $\omega_m = 0.984$).

We ranked the 64 possible models according to their Akaike information criterion corrected for small sample size (AIC_c) (Table S3) and restricted our candidate model set to models with $\Delta\ AIC_c < 4$ (30). For each model in the candidate set we calculated the Akaike model weight (ω_m), which reflects the probability that a model is the best approximating model given the set of candidate models considered (30). Marginal R^2 values (the variance explained by the fixed effects variables) of models were calculated following Nakagawa & Schielzeth (51). To account for model selection uncertainty we calculated full-model averaged parameter estimates (including zero when predictors were not included in a particular model (52)) for each predictor in the candidate model set. The relative importance (ω_p) of a predictor was based on the sum of the Akaike weights across all models in the candidate model set that included the predictor (30). All analyses were performed using R (53), using the packages "lme4" (54) and "MuMIn" (55).

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SUPPORTING INFORMATION

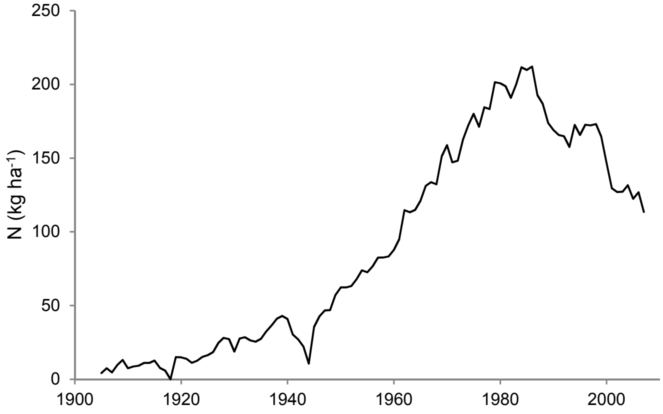

Figure S1. Average use of artificial nitrogen fertilizer per hectare of agricultural land in the Netherlands 1905-2007. Data was obtained from CBS Statistics Netherlands (http://statline.cbs.nl/statweb).

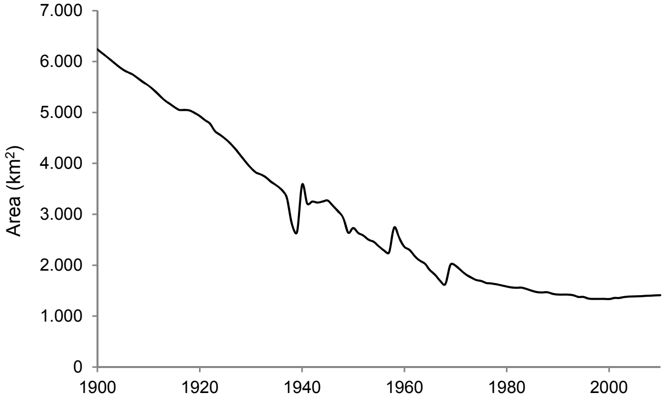

Figure S2. Area of open semi-natural habitat in the Netherlands 1900-2010. Data was obtained from CBS Statistics Netherlands (http://statline.cbs.nl/statweb).

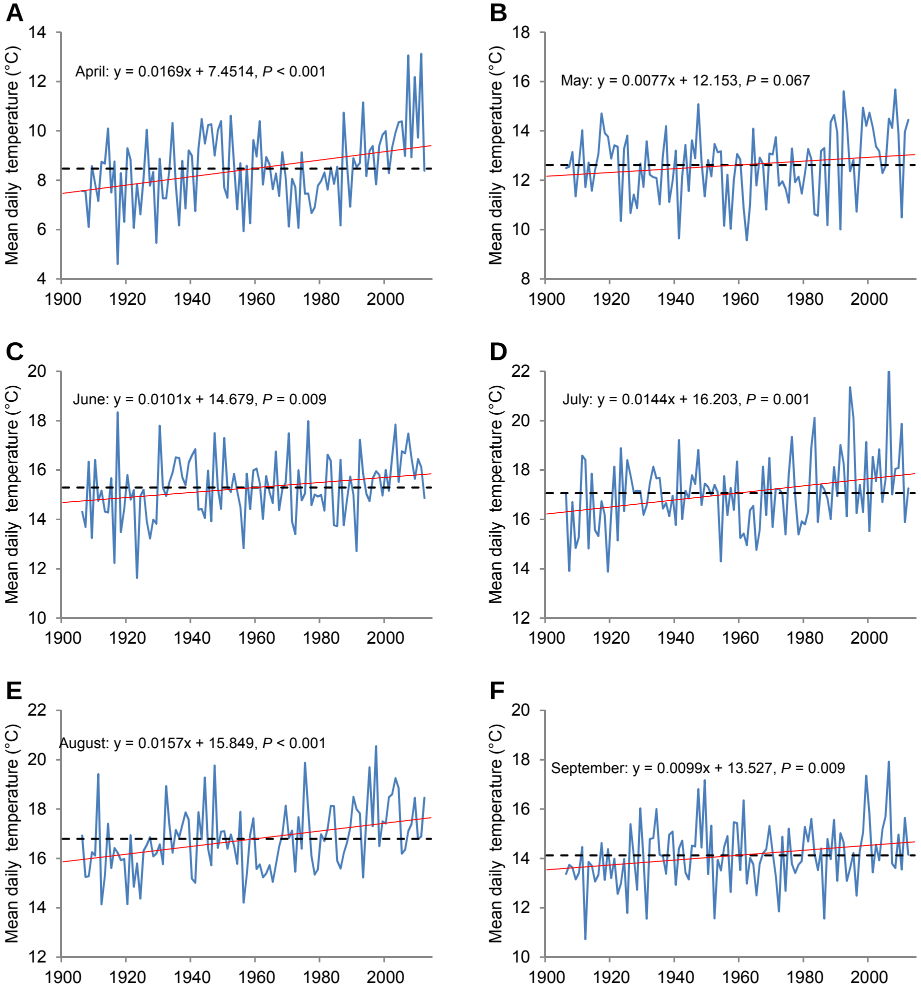

Figure S3. Mean daily temperature in the Netherlands 1906-2012. Trends in mean daily temperature (°C) during the months April (*A*) to September (*F*), covering the peak activity periods of most bee species. Linear regression lines indicate the changes in mean daily temperatures over the 107-year period. Data was obtained from the Royal Netherlands Meteorological Institute (KNMI) (http://www.knmi.nl/klimatologie).

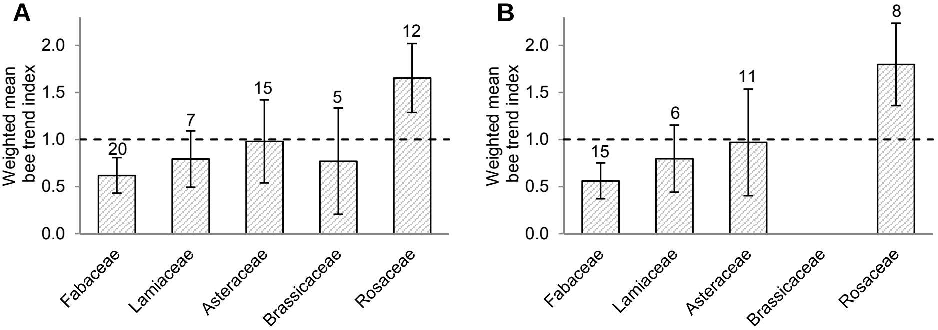

Figure S4. Weighted mean population trends of bee species visiting the most frequently used host plant families. Mean population trends, weighted by the percentage pollen contribution of the host plant families to bee species' diets, are calculated based on bee species for which a particular plant family contributed at least 20% (*A*) and 30% (*B*) to the pollen diet. Error bars indicate weighted 95% confidence intervals. Numbers above bars indicate sample size.

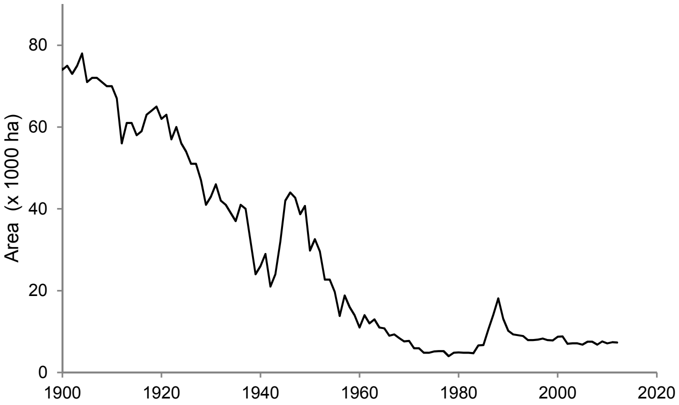

Figure S5. Area of Fabaceae crops in the Netherlands 1875-2012. Fabaceae crops include clover species (*Trifolium* spp.), alfalfa (*Medicago sativa*) and field beans (*Vicia faba*). Data was obtained from CBS Statistics Netherlands (http://statline.cbs.nl/statweb).

Table S1. List of bee species included in the analysis

Species	Subfamily	Change index	Species	Subfamily	Change index
Andrena barbilabris	*Andreninae*	1.59	*Bombus jonellus*	*Apinae*	0.28
Andrena bicolor	*Andreninae*	1.26	*Bombus lapidarius*	*Apinae*	0.60
Andrena carantonica	*Andreninae*	1.92	*Bombus pascuorum*	*Apinae*	0.61
Andrena chrysosceles	*Andreninae*	1.70	*Bombus pratorum*	*Apinae*	0.92
Andrena cineraria	*Andreninae*	0.94	*Bombus ruderatus*	*Apinae*	0.07
Andrena dorsata	*Andreninae*	1.20	*Bombus soroeensis*	*Apinae*	0.05
Andrena flavipes	*Andreninae*	2.12	*Bombus sylvarum*	*Apinae*	0.03
Andrena fucata	*Andreninae*	1.64	*Bombus terrestris*	*Apinae*	0.73
Andrena fulva	*Andreninae*	1.79	*Halictus confusus*	*Halictinae*	1.26
Andrena fulvida	*Andreninae*	0.43	*Halictus rubicundus*	*Halictinae*	1.43
Andrena gravida	*Andreninae*	0.62	*Halictus sexcinctus*	*Halictinae*	0.03
Andrena haemorrhoa	*Andreninae*	2.22	*Hoplitis claviventris*	*Megachilinae*	1.08
Andrena labiata	*Andreninae*	1.03	*Lasioglossum albipes*	*Halictinae*	1.26
Andrena nigriceps	*Andreninae*	0.38	*Lasioglossum calceatum*	*Halictinae*	1.39
Andrena nigroaenea	*Andreninae*	1.69	*Lasioglossum fulvicorne*	*Halictinae*	1.03
Andrena nitida	*Andreninae*	1.21	*Lasioglossum leucozonium*	*Halictinae*	2.32
Andrena ovatula	*Andreninae*	0.48	*Lasioglossum punctatissimum*	*Halictinae*	1.56
Andrena pilipes	*Andreninae*	0.25	*Lasioglossum sexnotatum*	*Halictinae*	0.80
Andrena semilaevis	*Andreninae*	0.95	*Lasioglossum sexstrigatum*	*Halictinae*	2.32
Andrena subopaca	*Andreninae*	1.99	*Lasioglossum zonulum*	*Halictinae*	1.38
Andrena tibialis	*Andreninae*	0.53	*Megachile centuncularis*	*Megachilinae*	0.72
Anthidiellum strigatum	*Megachilinae*	0.77	*Megachile circumcincta*	*Megachilinae*	0.30
Anthidium manicatum	*Megachilinae*	0.99	*Megachile leachella*	*Megachilinae*	0.82
Anthophora furcata	*Apinae*	0.68	*Megachile ligniseca*	*Megachilinae*	0.17
Anthophora plumipes	*Apinae*	1.29	*Megachile maritima*	*Megachilinae*	0.26
Anthophora quadrimaculata	*Apinae*	1.02	*Megachile willughbiella*	*Megachilinae*	1.57
Anthophora retusa	*Apinae*	0.22	*Osmia bicornis*	*Megachilinae*	1.44
Bombus hortorum	*Apinae*	0.74	*Osmia caerulescens*	*Megachilinae*	0.80
Bombus humilis	*Apinae*	0.11			

Table S2. Model selection and model averaging results for candidate models explaining bee population trends, based on the periods 1900-1989 and 1990-2001

	Model								
Predictor	1	2	3	4	5	6	β	95% CI	ω_p
Change of host plants	0.31	0.29	0.30	0.30	0.29	0.29	0.30	**0.08 to 0.52**	1.00
Body size	-0.44	-0.42	-0.42	-0.45	-0.41	-0.43	-0.43	**-0.67 to -0.19**	1.00
Range size before 1950	0.37	0.31	0.36	0.37	0.31	0.32	0.34	**0.14 to 0.27**	1.00
Diet breadth		0.16			0.15	0.16	0.06	-0.14 to 0.27	0.42
Length of flight period				-0.02		-0.01	0.00	-0.10 to 0.10	0.21
Phenological advancement			-0.08		-0.06		-0.01	-0.13 to 0.10	0.17
Δ AIC_c	0.00	0.57	2.06	2.60	2.99	3.29			
ω_m	0.36	0.27	0.13	0.10	0.08	0.07			

Candidate models are ranked in order of increasing differences in corrected Akaike information criterion (Δ AIC_c). Explanatory variables were standardized by centering and dividing by 2 standard deviations. Akaike model weights (ω_m) indicate the probability that a model is the best approximating model given the set of models considered. For each predictor the parameter estimate is given, along with its model averaged estimate (β) (including zeros for variables that are not in a particular model), 95% confidence interval, and relative importance (ω_p). Confidence intervals not overlapping zero are indicated in bold.

Table S3. Full set of models explaining bee population trends

Model ID	Change of host plants	Body size	Range size before 1950	Diet breadth	Length of flight period	Phenological advancement	AIC_c	Δ AIC_c
45	0.54	-0.63	0.29				82.0	0.00
46	0.53	-0.62	0.25	0.11			83.9	1.89
37	0.55	-0.51					84.2	2.21
38	0.53	-0.51		0.18			84.5	2.56
61	0.53	-0.64	0.30		-0.02		84.6	2.58
47	0.54	-0.63	0.28			0.01	84.6	2.60
53	0.58	-0.49			0.11		85.9	3.93
39	0.54	-0.52				0.09	86.1	4.15
40	0.52	-0.52		0.18		0.10	86.5	4.48
48	0.53	-0.62	0.24	0.11		0.03	86.5	4.56
62	0.52	-0.63	0.26	0.11	-0.02		86.6	4.57
54	0.55	-0.50		0.17	0.08		86.7	4.75
63	0.53	-0.64	0.29		-0.03	0.02	87.3	5.28
55	0.57	-0.50			0.09	0.06	88.4	6.37
56	0.53	-0.51		0.18	0.04	0.08	89.1	7.11
64	0.51	-0.63	0.25	0.11	-0.04	0.04	89.3	7.31
5	0.64						94.0	12.02
21	0.68				0.22		94.3	12.30
6	0.62			0.16			95.0	13.02
13	0.63		0.13				95.5	13.56
22	0.66			0.12	0.19		95.9	13.96
7	0.62					0.08	96.1	14.09
41		-0.79	0.31				96.1	14.13
29	0.67		0.05		0.20		96.7	14.70

Table S3 continued

23	0.68				0.22	0.00	96.8	14.80
57		-0.85	0.41		-0.20		96.9	14.94
8	0.60			0.16		0.08	97.1	15.13
14	0.61		0.08	0.13			97.2	15.21
42		-0.77	0.25	0.16			97.4	15.41
34		-0.66		0.23			97.5	15.49
33		-0.67					97.9	15.89
15	0.62		0.12			0.05	97.9	15.96
58		-0.83	0.35	0.16	-0.20		98.3	16.28
43		-0.79	0.29			0.07	98.4	16.42
24	0.65			0.12	0.19	0.02	98.5	16.55
30	0.66		0.01	0.12	0.19		98.5	16.56
36		-0.67		0.24		0.16	98.7	16.71
59		-0.86	0.38		-0.24	0.13	98.7	16.76
35		-0.68				0.15	99.2	17.17
31	0.67		0.05		0.20	-0.01	99.3	17.31
16	0.60		0.06	0.14		0.07	99.6	17.59
44		-0.76	0.22	0.17		0.09	99.6	17.62
50		-0.67		0.24	-0.07		99.8	17.77
60		-0.83	0.31	0.18	-0.25	0.16	99.8	17.82
52		-0.69		0.26	-0.16	0.22	100.2	18.25
49		-0.67			-0.03		100.2	18.25
51		-0.69			-0.11	0.19	101.2	19.20
32	0.65		0.00	0.12	0.18	0.02	101.2	19.26
1							106.7	24.72
2				0.21			106.9	24.90
3						0.17	107.7	25.75
4				0.22		0.17	107.9	25.91
9			0.17				107.9	25.91
17					0.09		108.8	26.78
10			0.10	0.18			108.9	26.92
18				0.21	0.04		109.2	27.24
11			0.12			0.13	109.6	27.58
19					0.02	0.16	110.1	28.15
25			0.16		0.01		110.3	28.32
12			0.04	0.20		0.16	110.3	28.35
20				0.22	-0.04	0.18	110.4	28.38
26			0.10	0.18	0.00		111.4	29.43
27			0.14		-0.04	0.14	112.0	30.04
28			0.06	0.21	-0.06	0.17	112.9	30.86

Candidate models (Δ AIC_c < 4) used for model averaging are indicated in grey. Explanatory variables were standardized by centering and dividing by 2 standard deviations.

CHAPTER 3

Does conservation on farmland contribute to halting the biodiversity decline?

David Kleijn[1], Maj Rundlöf[2,3], Jeroen Scheper[1],
Henrik G. Smith[2] & Teja Tscharntke[4]

[1]Alterra, Centre for Ecosystem Studies, Droevendaalsesteeg 3, P.O. Box 47, 6700 AA, Wageningen, The Netherlands; [2]Department of Biology & Centre for Environmental and Climate Research, Lund University, SE-223 62 Lund, Sweden; [3]Department of Ecology, Swedish University of Agricultural Sciences, P.O. Box 7044, SE-75007 Uppsala, Sweden; [4]Agroecology, University of Göttingen, Waldweg 26, D-37073 Göttingen, Germany.

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Abstract

Biodiversity continues to decline, despite the implementation of international conservation conventions and measures. To counteract biodiversity loss, it is pivotal to know how conservation actions affect biodiversity trends. Focussing on European farmland species we review what is known about the impact of conservation initiatives on biodiversity. We argue that the effects of conservation are a function of conservation-induced ecological contrast, agricultural land-use intensity and landscape context. We find that to date hardly any studies have linked local conservation effects to national biodiversity trends. It is therefore unknown how the extensive European agri-environmental budget for conservation on farmland contributes to the policy objectives to halt biodiversity decline. Based on this review, we identify new research directions addressing this important knowledge gap.

Actions to reverse biodiversity decline

In 1992, 168 countries committed to the conservation of biodiversity by signing the Convention on Biological Diversity (CBD). In 2002, in what has been called the most significant conservation agreement of the early 21st century [1], world leaders set the concrete goal of achieving a significant reduction in the rate of biodiversity loss by 2010 [2]. Important tools with which this was to be achieved included a wide range of international treaties (e.g. Convention on International Trade in Endangered Species, Convention on Migratory Species, Ramsar Convention) and various policy tools such as the EU Nitrates Directive, Natura 2000 (EU Birds and Habitats Directives) and agri-environment schemes. With the passing of the year 2010, however, it has become clear that these treaties and instruments have been insufficient means to reach this target [3]. Between 1970 and 2009, conservation efforts increased rapidly and significantly, but biodiversity threats increased as well. To understand why biodiversity is still declining it is pivotal to know how conservation actions and threats interact and ultimately to what extent conservation can counteract biodiversity loss.

Focussing on European farmland species, this paper reviews and discusses what is known about the impact of conservation policy tools on biodiversity. In Europe more than 45 % of the countryside is used as farmland [4] and many threatened species are strongly associated with farmland habitats. The decline of this group of species is well-documented and particularly steep [5]. The drivers of this decline have been examined extensively and are relatively well-understood [6-9]. Species from other parts of the world and from more natural habitats are only now beginning to receive a similar level of attention [10 – 12]; in contrast, the effects of conservation policy tools on European farmland have been examined extensively for more than a decade.

Mixed effects of farmland biodiversity conservation

Biodiversity conservation on farmland encompasses of a wide range of different measures. Many measures aim to enhance biodiversity by restricting farming intensity, for example by restricting stocking rates or agrochemical inputs. Other measures aim to maintain low-input farming practices by preventing intensification or farmland abandonment. Yet other measures promote the maintenance or creation of landscape elements such as hedges, ponds or wildflower strips. In Europe, many of these measures are subsidized in the framework of agri-environment schemes. Outside Europe, similar schemes exist, such as the USA Conservation Reserve Program or the largely unsubsidized Australian Landcare Program [91]. The term 'biodiversity conservation initiatives on farmland' used in this paper refers to the entire range of tools and initiatives, both subsidized and voluntary. However, each EU member state is obliged to establish an agri-environmental program. As a result, the EU 2007-2013 budget for agri-environment schemes is €34.5 billion [13], and literature on this type of initiative dominates.

Since 2000, a large number of studies from various European countries have examined the effects of conservation initiatives on farmland [14-21, see online Supplementary Material Appendix 1 for the type of conservation initiatives that were considered]. Most studies examining the effects of conservation initiatives on farmland compare biodiversity on sites with low-input, nature-friendly management with that on control sites that are managed following conventional agricultural practices. In this paper, we therefore similarly consider ecological effects of conservation initiatives to be the difference in a biodiversity variable (usually species richness or abundance) between sites with conservation management and control sites. So far, the rapidly expanding body of literature suggests that biodiversity conservation on farmland has mixed effects [16,19,22]. Some initiatives enhance biodiversity [23-25] whereas other initiatives fail [17,26,27]. The effect of one single conservation measure can even differ between regions [28,29].

Current hypotheses explaining conservation effects on farmland

Two hypotheses have been put forward to explain the variable effectiveness of conservation initiatives on farmland. Kleijn & Sutherland [16] proposed what might be called the land-use moderated conservation effectiveness hypothesis. This hypothesis predominantly focuses on within-field processes and has its basis in competition and niche theory and intermediate-disturbance theory [30-32]. Extensively managed, low-input farmland is generally characterized by high within-field spatial heterogeneity [33] and low rates of disturbances caused by cutting or grazing, pesticide applications or soil cultivation. In such systems, many different species can occupy many different available niches or habitats. Furthermore, many species can reproduce successfully in the time between two disturbances thereby sustaining viable populations. Agricultural intensification results in increased agricultural specialization (reduction in the number of available ecological niches), increased use of external inputs and increased disturbance rates. With increasing intensification, fewer and fewer species will therefore be able to compete and reproduce successfully in the few remaining crops, under the nutrient-rich conditions and in the short time-intervals between two disturbances [34]. Because of the additive effects of the many correlated disturbances (land-use intensity variables), biodiversity on agricultural land declines exponentially with increasing land-use intensity [8]. This particular relationship suggests that conservation will be most effective in extensively farmed agricultural areas because here the potential biodiversity increase per land-use intensity change will be highest [8,16]. This hypothesis has not yet been tested, but recent results of Batáry et al. [35] are in line with it.

While the land-use moderated conservation effectiveness hypothesis mainly considers management activities on farmland, the second hypothesis takes the wider countryside into perspective. The landscape moderated conservation effectiveness hypothesis [36] has its basis in meta-community theory [37,38]. Tscharntke et al. [36] argue that population persistence of farmland species depends on continuous colonization and extinction processes in both crop and non-crop habitats. Complex landscapes consist of a mosaic of different habitats in which population colonization and extinction rates of many different species are balanced, thus supporting high overall biodiversity. In simple landscapes, agricultural land dominates and semi-natural habitats are isolated. This is hypothesised to make extinction the dominant population process with a consequent lowering of biodiversity levels. Based on this concept, Tscharntke et al. [36] predicted that the effectiveness of conservation initiatives on farmland is highest in structurally simple landscapes (2-20% semi-natural habitats in the matrix) because here species sources are still present (unlike in ‘cleared’ landscapes with less than 2% semi-natural habitats) and biodiversity on intensively managed fields is not subsidized by the continuous colonization of species from the surrounding species-rich landscape (such as in complex landscapes with more than 20% semi-natural habitats). The findings of an increasing number of studies indicate that conservation effectiveness, i.e. the difference in species richness between sites with and without conservation initiatives, is indeed higher in simple than in complex landscapes [25,28,39-42]. Nevertheless, landscape structure does not always seem to influence the effectiveness of conservation initiatives on farmland [43] and a recent meta-analysis of Batáry et al. [44] shows that moderating effects of landscape structure on conservation benefits differ between grasslands and arable lands and vary between functional species groups.

Obviously, the effectiveness of conservation initiatives cannot be exclusively explained by one or the other hypothesis. To begin with, the effects of conservation initiatives depend on the type of measures that are being implemented and to what extent they improve habitat conditions for the targeted species group relative to conventionally managed habitat. In other words, how large is the 'ecological contrast' created by the initiative. The response of biodiversity to this ecological contrast will subsequently be moderated by land-use intensity and landscape structure (see Box 1). This offers one explanation of why the outcomes of evaluation studies vary markedly between different schemes, regions and countries. Another explanation may be the many different ways in which both land-use intensity and landscape complexity are being measured (see Online Supplementary Material Appendix 1).

Conserving what is left is more effective than getting back what was lost

Both hypotheses address improvement effects of conservation initiatives, that is, their potential to increase biodiversity through agricultural change. An aspect that is only partially considered by these hypotheses is the 'protection effect' of conservation initiatives. Protection effects indicate effects of conservation initiatives that *prevent loss of biodiversity* through agricultural change [48]. It can be quantified as the difference in species richness between a conventionally farmed site where technological and socio-economic developments are resulting in more intensive management and a site where conservation initiatives are maintaining traditional extensive agricultural management. However, protection effects of farmland conservation initiatives also include prevention of agricultural abandonment. In many areas in Europe, the extensive management of agriculturally marginal but species-rich sites is economically unviable and these areas are only being maintained by being subsidised by green-farming schemes [49]. Agricultural abandonment generally results in a decline in

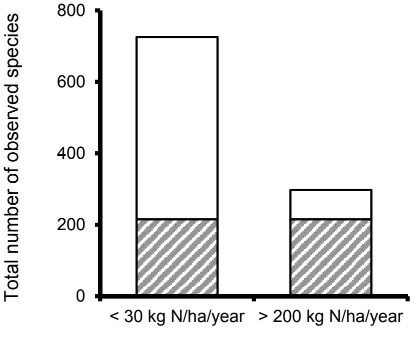

Figure 1. The difference in the total number of observed plant species on 65 extensively [characterised by nitrogen (N) input of < 30 kg N/ha/year] and 65 intensively (>200 kg N/ha/year) farmed fields that were surveyed in 2003 in six European countries. Open bars indicate species numbers unique to extensive or intensive fields, shaded bars indicate species numbers that extensive and intensive fields had in common. For more detailed information on sampling approach, see Kleijn et al. [8] from which the data were obtained.

Box 1. Conservation effects moderated by land-use intensity, landscape structure and ecological contrast

Biodiversity is not linearly related to land-use intensity [8]. A certain reduction in land-use intensity therefore results in larger potential effects in low-input farming systems than in high-input farming systems, for example, because in such areas even with conservation management the high intensity level prohibits the colonization of new species even if source populations are nearby [45, Figure Ia,e]. A reduction in land-use intensity is more effective in low-input farming systems than in no-input farming systems where further agricultural extensification, if possible, is not likely to increase biodiversity [35]. This suggests that initiatives have the highest conservation potential if they are being implemented on agricultural land that is already being managed relatively extensively or where biodiversity friendly management reduces land-use intensity to this low-intensity level.

Of course, effectiveness of conservation also depends on the extent to which management improves habitat conditions for the targeted species group relative to conventionally managed habitats. This can be considered the ‘ecological contrast’ created by conservation initiatives (i.e. compare arrows along the X-axes in Figures Ia and Ie). Conservation initiatives resulting in large ecological contrasts will be more effective than conservation initiatives resulting in small contrasts and can effectively be implemented in a wider range of land-use intensities. For example, to enhance the diversity and abundance of bumblebees, providing a mixture of preferred flowering plant species [46] is more effective than delaying the mowing date of species-poor Dutch agricultural grasslands (47].

At the same time, the effectiveness of conservation initiatives is moderated by landscape context (Figures Ib-d, f-h). Conservation has more pronounced effects in structurally simple landscapes (2-20 % semi-natural habitats) than in structurally complex landscapes (>20% semi-natural habitats). For example, because in landscapes with high overall species richness and abundance, many individuals will spill-over from the surrounding landscape onto conventionally managed fields. This might obscure differences between sites with conservation initiatives and control sites [40]. Likewise, conservation has more pronounced effects in simple landscapes compared to landscapes devoid of semi-natural habitats (<2 %) because in landscapes lacking potential colonizers, even conservation initiatives that considerably improve site conditions will fail to enhance species numbers.

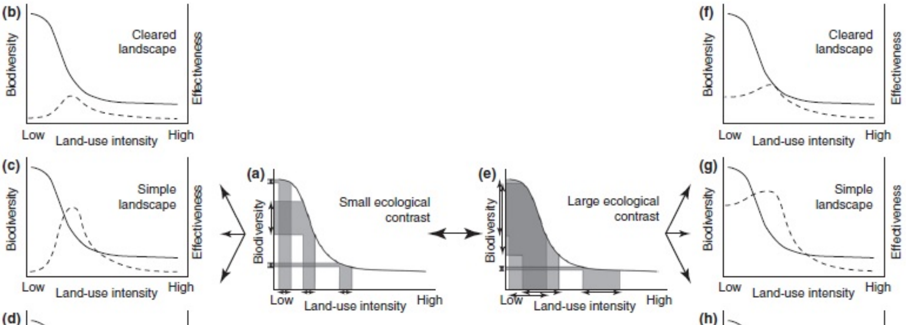

Figure I. A conceptual model of how the potential effects of conservation initiatives on farmland are moderated by land-use intensity, landscape structure and the ecological contrast created by the con-servation initiatives (here indicated as reduction in land-use intensity). Solid lines indicate biodiversity, dashed lines indicate effectiveness. Effectiveness indicates the difference in biodiversity between sites with conservation management and conventionally managed sites. In contrast to Kleijn et al. [8] here we use a truncated hump-shaped relationship between land-use intensity and biodiversity to include a wider range in land-use intensity than that examined by Kleijn et al. [8] so that agricultural systems that do not use external inputs (but might nevertheless be used more or less intensively [35,90]) are taken into account.

(farmland) biodiversity [50,51] so conservation initiatives preventing this will contribute significantly to biodiversity conservation. This aspect of farmland conservation initiatives lies outside the framework presented in Box 1 but is particularly important because agriculturally marginal areas such as parts of Central and Eastern Europe, the Mediterranean or the Alps still host particularly high levels of biodiversity.

Box 2. Different conservation objectives require different implementation strategies

It is useful to distinguish between objectives of farmland conservation initiatives that address the intrinsic value of biodiversity and objectives that address functional aspects of biodiversity [53,54]. Intrinsic objectives of conservation generally address absolute criteria (the conservation of all possible species that could be sustained by a site) or relates to species identity (the promotion of rare or endangered species). Conservation initiatives with intrinsic biodiversity objectives should focus on the very to moderately extensively managed and structurally complex areas (Table I) because in these areas biodiversity is still high and endangered species occur in large numbers and high densities and conservation therefore has the highest potential protection effect. Conservation initiatives should be implemented both at the local level (prevent intensification of agricultural management) and at the landscape level (maintaining a diversity of habitats). Only if particular endangered species are occurring on more intensively managed land it can be worthwhile to implement conservation measures in such areas [15, Table I].

Conservation objectives addressing functional aspects of biodiversity generally target the services biodiversity provides such as crop pollination [55,56] or pest control [57,58]. Conservation initiatives with functional objectives should be targeted at more intensively farmed areas because in these areas ecosystem services are likely to be reduced due to the intensive farming practices. Furthermore, here the use of external inputs and crop yields is higher than in agriculturally marginal areas making the potential benefits (e.g. due to reduced pesticide applications or improved crop yields) of conservation-induced increases in ecosystem services higher. Such functional biodiversity conservation initiatives should preferentially be implemented in structurally simple landscapes as here the largest benefits can be expected [Table I, 36]. Rare or endangered species probably play a minor functional role in ecosystems so their general absence from more intensively farmed landscapes should not affect the provision of ecosystem services.

Currently, conservation initiatives on farmland rarely have clearly defined biodiversity objectives [16,22,54]. It is unlikely that objectives addressing the intrinsic value and functional aspects of biodiversity can easily or effectively be combined [54,59]. Effective biodiversity conservation on farmland therefore requires clarity about what kind of biodiversity should be conserved or enhanced by conservation initiatives.

Table I Implementation criteria and management recommendations that optimize the effectiveness of conservation initiatives on farmland with different biodiversity objectives.

Intrinsic biodiversity values	**Ecosystem services**
Implementation criteria	
In agriculturally marginal areas	In agriculturally profitable areas
In structurally complex landscapes	In structurally simple landscapes
In areas with high levels of biodiversity	In all areas except for the most species-rich or species-poor
In areas with rare or endangered species	Independent of species identity
Near source populations of target species	Independent of source populations
Management recommendations	
Maintain traditional management on agriculturally marginal land	Reduce management intensity on intensively farmed land
Implement measures specifically targeted to rare/endangered species (often requiring significant changes in farming activities)	Implement general measures (requiring little change in farming activities)

Furthermore, agriculturally marginal areas generally also host the highest number and abundance of endangered species [51, 52]. While there are many species adapted to the extensive farming practices that were once dominant throughout Europe, there are no species characteristic of the intensive practices of modern-day Western European agriculture. For example, a survey of agricultural plant communities in six European countries with contrasting management intensity revealed that 72 % of the species found on intensively farmed fields were also found on extensively farmed fields where they represented only 30 % of the total number of species observed (Fig. 1). Moreover, five of the top ten most frequently observed plant species were the same for extensively and intensively farmed fields: Couch grass (*Elymus repens)*, Dandelion (*Taraxacum officinale)*, Rough meadowgrass (*Poa trivialis)*, White clover (*Trifolium repens)* and Knotgrass (*Polygonum aviculare)*. Intensification therefore does not result in a shift from one species community to another. Rather, it results in the dominant species becoming even more dominant and the rare species going extinct.

The differentiation between protection and improvement effects in combination with the restricted occurrence of rare species in particular agricultural landscapes suggests that it is important to consider the reason why one wants to conserve biodiversity on farmland. Conservation initiatives targeted at rare species or high diversity levels should be implemented in different landscapes or areas and using different approaches than initiatives aiming to increase biodiversity because of the services it delivers (Box 2).

Limitations of current evaluation approaches

The increasing number of studies examining the effects of conservation initiatives on farmland have revealed a number of weaknesses of the most widely used evaluation methods. Most studies use species-richness or abundance as an indicator of biodiversity effects (see Online Supplementary Material Appendix 2). Assuming that conservation initiatives do, as intended, lead to the creation of higher quality sites and that conventionally managed farmland represents poor quality sites, a number of related ecological phenomena can hamper a straight-forward interpretation of effectiveness studies that use species richness of abundance as response variables [60,61].

First, density dependent processes such as source-sink dynamics [62] and buffer effects [63] can obscure qualitative differences between fields or habitat types. Source-sink dynamics describe a phenomenon where breeding populations in low-quality habitats (sinks) are supported by an immigration flux from (nearby) breeding populations in high-quality habitats (sources). Under such conditions, a comparison of abundance or species-richness overestimates the suitability of the low-quality site, and underestimates the suitability of the high-quality site. Buffer effects describe a similar phenomenon outside the breeding season. It occurs when sites vary in quality and fluctuations in population size are accompanied by large changes in animal numbers in poor-quality sites and small changes in good-quality sites [63]. In growing populations this might lead to animal numbers on poor-quality sites increasing more rapidly than on high-quality sites which would again result in an overestimation of low-quality and an underestimation of high-quality sites in studies using species richness or abundance to compare site quality.

Second, small-scale spatio-temporal processes can obscure differences in habitat quality created by conservation initiatives. Regardless of their suitability, agricultural fields will be colonized by random or deliberate dispersal of individuals from nearby semi-natural habitats [64-66]. These so-called spill-over effects can overrule any patterns in species-richness or abundance created by conservation initiatives [67]. Spill-over effects generally act at relatively small spatial scales (< 300 m [65,66]) suggesting they are particularly important in small-scaled, and less so in large-scaled agricultural landscapes. This is one mechanism that could give rise to the often observed higher effectiveness of conservation initiatives in simple compared to complex landscapes (Box 1, [36]). The effectiveness of conservation initiatives is furthermore generally measured during the peak of resource provisioning (e.g. peak standing crop, main flowering season). It is unknown whether the differences measured at that time are representative for differences at the end of the season or the beginning of the next season. For example, the cultivation of oil seed rape (*Brassica napus*) was found to enhance the densities of workers of the Buff-tailed bumble bee (*Bombus terrestris*) but did not enhance reproductive success [68]. Concentration responses are another type of small-scale spatio-temporal processes that can influence the outcome of comparisons of sites with conservation management and conventionally farmed sites. While concentration responses have rarely been documented directly, a number of recent studies have found that resource-rich patches have a more positive effect on species richness and abundance in resource-poor than in resource-rich landscapes [25,69-71]. In theory, this could indicate that in resource-poor landscapes, resource-rich patches are supporting more species or individuals than in resource-rich landscapes. A more likely explanation is that this response is caused by a stronger concentration of the local pool of individuals on the few resource patches in resource-poor landscapes than on the many resource patches in resource-rich landscapes. Like spill-over effects this response could give rise to the higher apparent effectiveness of conservation initiatives in simple compared to complex landscapes (Box 1, [36]).

Third, species might be able to initially survive habitat change but, without any subsequent habitat improvement, become extinct eventually [72]. This phenomenon, known as extinction debt [73], probably explains the current persistence of farmland bird species in many intensively farmed areas in Western Europe. Here, survival and reproductive success is often too low to maintain stable populations [74], which is illustrated by the rapidly declining populations of farmland birds in most Western European countries [75]. Without any interventions or positive land-use changes many of these species will go extinct in the near future on conventionally managed agricultural land on which they are currently still abundant. Extinction debt might therefore result in an underestimation of the difference in habitat quality between sites with conservation initiatives and those that are conventionally managed, especially in species with long generation times, in populations near their extinction threshold and shortly after habitat modification when this phenomenon is most likely to occur [72].

When the potentially confounding effects of the previously discussed ecological processes are not considered in empirical field studies that compare species-richness on fields with conservation initiatives with that on control fields, it is hazardous to equate differences in species richness or abundance with effects of conservation initiatives. In general, responses of animals to plot- or field level treatments are a poor indication of the population response at the landscape level with the possible exception of species groups whose movements in and out of the treated area are relatively limited [76]. Whether or not to use such an approach depends ultimately on the objectives of the conservation initiatives (Box 3).

Box 3 Different conservation objectives require different evaluation approaches

When considering what study design is most suitable for evaluating farmland conservation initiatives it is important to distinguish between initiatives aiming to enhance biodiversity as such and initiatives aiming to enhance biodiversity for the ecosystem services it provides. If biodiversity's intrinsic values are the primary motivation for conservation, initiatives resulting in behavioural responses without any additional population level responses should be considered ineffective. For the provision of ecosystem services, on the other hand, behavioural responses can be just as important as population level responses. For example, for the effectiveness of pollination, the reason why a pollinator is available to pollinate a crop is irrelevant. This suggests that the methodologies with which conservation initiatives are being evaluated should consider the objectives of these initiatives. Straight-forward studies of differences in species-richness or abundance between sites with and without conservation management are less suitable for evaluating initiatives which aim to conserve biodiversity for its own sake than for initiatives in which biodiversity is an intermediary of ecosystem services.

From conservation action to policy objectives

When we compare the insights presented in this paper with those in reviews that were made not long ago [16,18] it is clear that our understanding of the effectiveness of conservation initiatives on farmland has vastly improved during the last few years. Nevertheless, the question how farmland conservation initiatives have contributed to the policy objectives of halting the biodiversity decline has yet to be addressed. The best available efforts to date have studied the impact of agri-environment schemes on birds in the UK. The range restricted UK Cirl bunting (*Emberiza cirlus*) population increased markedly due to the provision of grass margins and weedy winter stubbles [15]. A recent study [93] suggests that the decline of the Scottish Corn bunting (*E. calandra*) could be reversed if 72% of that population received targeted agri-environment schemes.

The mismatch of conservation evaluation studies and conservation policy objectives may be due to them being implemented at different spatial scales. Policy objectives are generally formulated at the national or even continental level [77,78]. Conservation initiatives, on the other hand, are taken at the field, site or farm level, which is also the typical spatial scale of evaluation studies. Species-area relationships can be used to link biodiversity trends to land-use change [79]. This approach is, however, based on assumptions that the landscape matrix is completely inhospitable to the species of interest and that fragmentation effects do not factor into extinction risk [80] which are both unrealistic for farmland species. Because species-area relationships are non-linear and differ between habitats we are not yet able to scale up the effects of locally implemented conservation initiatives to larger spatial scales. Studies comparing species-richness on sites with and without conservation initiatives can therefore not be used to inform us how conservation actions contribute to conservation policy objectives.

Furthermore, the approach of most evaluation studies to compare biodiversity between two habitat types (such as conventional and nature-friendly farmed land) ignores the fact that during their life cycle most farmland species depend critically on habitats other than these two. For example, in Europe the Farmland Bird Indicator is being used as an indicator of farmland health [78]. However, several of the species that are the basis of this indicator are migrants that breed and winter in different countries or even continents. Population trends are therefore not only dependent on the quality of the breeding habitat but also on the conditions in the wintering habitat [81]. Similarly, population dynamics of many bee species is not only constrained by food availability, lack whereof is often mitigated in conservation initiatives [46] but also by nest site availability [82] which, because few bee species nest on farmland, is generally not addressed by conservation measures on farmland. Positive spatio-temporal effects of conservation initiatives on agricultural fields can therefore easily be offset by negative spatio-temporal effects of land-use change in the wider countryside [83]. Because most species are influenced by factors at the landscape level as well as at the field level this highlights the importance of a landscape scale perspective for conservation initiatives as well as for studies evaluating these initiatives.

Box 4 The way forward

The field of farmland conservation biology is rapidly developing. New technologies become available that can be used to answer previously unaddressable questions. For example, the increasingly small size of satellite and radio transmitters and gps-loggers depict landscape use of an increasing number of farmland species thereby allowing us to identify spatial scales relevant for conservation action [87]. New statistical techniques are being developed that are giving us a much better understanding of the ecological implications of what we observe and measure [88]. Easily applicable molecular techniques are allowing us to estimate genetic diversity and population size of more and more species [92]. The most pressing questions that need to be tackled if we want to better understand the ecological effects of conservation initiatives on farmland and how they contribute to the conservation objectives of policy makers are:

1. What are the effects of conservation initiatives on the demography and population dynamics of species?
2. How do effects of local conservation initiatives scale up to national or continental biodiversity trends?
3. What part of species richness responses to conservation initiatives are caused by behavioural responses and what part by population level responses?
4. How significant are effects of conservation initiatives compared to effects of land-use change resulting from autonomous processes (e.g. the introduction of new (varieties of) crops, new harvesting techniques, ongoing intensification) in the wider countryside that is used by the target species?

It is perhaps surprising that so far hardly any study has related conservation initiatives to national population trends of the target species. The contribution of local conservation initiatives to national biodiversity objectives can be assessed in a relatively straight-forward fashion using a demographic approach. Studies of the demographic effects of conservation management can take into account the impact of the surrounding landscape, can differentiate between life stages and reproductive and non-reproductive stages and, importantly, can be scaled up to higher spatial scales. Such approaches have been applied to address a variety of questions including the large-scale impact of climate change on Polar bear (*Ursus maritimus*) populations [84], the impact of hunting on geese species [85], or the impact of fire regimes on the persistence of plant populations [86] but have so far not been used to assess the impact of conservation initiatives on farmland. The down side of the demographic approach is that it requires detailed information (and can therefore be costly). Demographic responses to conservation management are influenced by landscape structure and land-use intensity and therefore require data from the entire range of landscape types for which future projections need to be made. Furthermore, the demographic approach does not yield information on the diversity produced by conservation management. However, if applied to one or a few representative species and accompanied by more traditional biodiversity studies this approach could significantly advance our understanding of the large-scale impact of local conservation initiatives (Box 4).

Conclusions

Currently, there is a general awareness amongst conservationists as well as policy makers that, despite clear targets and objectives and increasing conservation efforts, we have failed to halt the decline of biodiversity. This paper shows for farmland biodiversity that it is generally unknown if and how conservation efforts have moderated this decline (but see [10]). It is unknown how the policy tools to counteract biodiversity decline contribute to the policy objectives for which they were (at least partially) designed. The EU has recently agreed on a new long-term (2050) vision and mid-term (2020) headline target for biodiversity in the EU. The aim is to halt the loss of biodiversity and the degradation of ecosystem services in the EU by 2020, restore them in so far as feasible, while stepping up the EU contribution to averting global biodiversity loss (EU Regulation 7536/10). The EU ‘stresses the need for an ambitious science-based 2011-2020 Strategic Plan, which sets a clear logical framework of goals, strategic, measurable, achievable, realistic and time-bound targets and associated indicators’ [89]. The current review suggests that these indicators should be chosen in such a way that they can link conservation action to biodiversity targets. Impact of conservation strategies should be monitored within the context of land-use in the wider countryside and in such a way that effects can be scaled up to national or continental biodiversity trends. In other words, we should make sure that in 2020, unlike in 2010, we will be able to tell how conservation initiatives have contributed to the biodiversity targets that are being set by us now.

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SUPPLEMENTARY MATERIAL

Does conservation on farmland contribute to halting the biodiversity decline?: Online Appendix 1. Notes on the type of conservation initiatives considered in this review and the impact of varying definitions of land-use intensity and landscape structure on the outcome of studies evaluating the effect of conservation initiatives on farmland.

David Kleijn, Maj Rundlöf, Jeroen Scheper, Henrik G. Smith, Teja Tscharntke.

Type of conservation initiatives considered

Although the primary objective of some of the examined conservation initiatives is not always biodiversity conservation (e.g. set-aside, organic farming, game cover strips) they have in common that they relax the intensity of land-use on farms or (parts of) agricultural fields and have, at times, proven to be beneficial to biodiversity. They are therefore included when we refer to conservation initiatives on farmland.

Landscape structure, land-use intensity, definitions and outcome of evaluation studies

Agricultural intensification generally results in a simplification of the agricultural landscape [A1.1, A1.2] and to some extent land-use intensity and landscape structure will be correlated. This relationship is, however, by no means robust and further depends on how and at what spatial scale land-use intensity or landscape structure is being measured [A1.3]. For example, Central European grasslands such as pusztas are characterized by large fields consisting of only a few habitat types. If habitat diversity is used as an indicator of landscape complexity [A1.4] these landscapes qualify as simple. These species-rich agricultural fields generally receive little or no fertilizers or pesticides [A1.5]. Management is therefore similar to that in many north-western European nature reserves which are generally considered to be semi-natural habitats. If the percentage of semi-natural habitats is used as an indicator of landscape complexity [A1.6], pusztas qualify as being quite complex. The many different ways of measuring both land-use intensity and landscape structure offer another explanation for the contrasting results of different studies examining the effects of conservation initiatives on farmland.

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Does conservation on farmland contribute to halting the biodiversity decline?: Online Appendix 2. The most frequently used response variables in studies that examine the effects on pollinators of conservation initiatives on farmland.

David Kleijn, Maj Rundlöf, Jeroen Scheper, Henrik G. Smith, Teja Tscharntke.

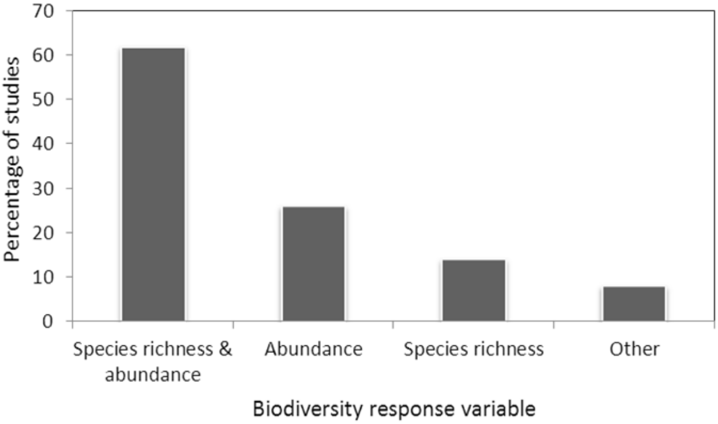

Figure A.1. The most frequently used response variables in biodiversity studies that examine the effects on pollinators of conservation initiatives on farmland. Relevant peer-reviewed papers were searched in ISI Web of Science (2010) and Scopus. Search phrases that were used were '(pollinat* OR apoidea OR bee OR butterfl* OR Lepidoptera OR hoverfl* OR Syrphidae) AND (agri-environment* OR mitigation OR "organic farming" OR management OR conservation OR restoration OR "field margin" OR "nature reserve" OR "flowering crop" OR "protected area" OR "field edge" OR set-aside)'). A total of 96 papers were obtained that were relevant for the purpose of this study. Almost all studies examined species richness, abundance or both. Response variables in studies that examined 'other' variables usually examined a population dynamical variable (often in combination with species richness and/or abundance).

CHAPTER 4

Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis

Jeroen Scheper[1], Andrea Holzschuh[2], Mikko Kuussaari[3], Simon G. Potts[4],
Maj Rundlöf[5], Henrik G. Smith[5] & David Kleijn[1,6]

[1]Alterra, Animal Ecology Team, PO Box 47, 6700 AA, Wageningen, The Netherlands; [2]Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am Hubland, 97074 Würzburg, Germany; [3]Finnish Environment Institute, Natural Environment Centre, Ecosystem Change Unit, P.O. Box 140, FI-00251 Helsinki, Finland; [4]School of Agriculture, Policy and Development, University of Reading, Reading, RG6 6AR, UK; [5]Department of Biology & Centre of Environmental and Climate Research, Lund University, S-223 62 Lund, Sweden; [6]Resource Ecology Group, Wageningen University, Droevendaalsesteeg 3a, 6708 PD, Wageningen, The Netherlands

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Abstract

In Europe agri-environmental schemes (AES) have been introduced in response to concerns about farmland biodiversity declines. Yet, as AES have delivered variable results, a better understanding of what determines their success or failure is urgently needed. Focusing on pollinating insects, we quantitatively reviewed how environmental factors affect the effectiveness of AES. Our results suggest that the ecological contrast in floral resources created by schemes drives the response of pollinators to AES but that this response is moderated by landscape context and farmland type, with more positive responses in croplands (vs. grasslands) located in simple (vs. cleared or complex) landscapes. These findings inform us how to promote pollinators and associated pollination services in species-poor landscapes. They do not, however, present viable strategies to mitigate loss of threatened or endangered species. This indicates that the objectives and design of AES should distinguish more clearly between biodiversity conservation and delivery of ecosystem services.

INTRODUCTION

Farmland, covering 47% of the EU-27 area (EEA 2010), has traditionally supported high levels of biodiversity in Europe (Bignal & McCracken 1996). However, the intensification of agriculture since the second half of the 20th century has caused severe declines in farmland biodiversity (Benton *et al.* 2003), which may impact on the delivery of ecosystem services (Balvanera *et al.* 2006). In response to increasing concern about the loss of farmland biodiversity, agri-environmental schemes (AES) have been introduced in Europe in the early 1990s. AES provide financial incentives to farmers for adopting agri-environmental measures that, among other objectives, aim to enhance biodiversity on farmland, and are currently seen as an important tool to halt or reverse negative biodiversity trends. Yet, the effectiveness of AES in the conservation of biodiversity has been debated (Kleijn & Sutherland 2003) and results of studies evaluating the effectiveness of AES have been mixed (Kleijn *et al.* 2006; Blomqvist *et al.* 2009; Wilkinson *et al.* 2012). In the sense that the 2010 target of the European Union to halt biodiversity loss on farmland have not been met (EEA 2010), it can be argued that AES have generally failed in meeting the biodiversity objective. Therefore, as biodiversity continues to decline, it is pivotal to know what ecological factors explain success or failure of agri-environmental measures.

Several ecological theories have been proposed to explain the variable effectiveness of agri-environmental measures in mitigating biodiversity loss. Effectiveness, i.e. enhancement of biodiversity in sites under agri-environmental management compared to control sites, has been hypothesized to be influenced by a number of factors. First, Tscharntke *et al.* (2005) hypothesized that effectiveness is influenced by landscape context and the size of the landscape-wide species pool. Based on meta-community theory, they predicted that effects of agri-environmental measures should be more pronounced in structurally simple landscapes (1-20% semi-natural habitats) than in cleared (<1% semi-natural habitats) or complex landscapes (>20% semi-natural habitats). In complex landscapes, mosaics of agricultural and semi-natural habitats support large species pools and effects of AES may be (partly) concealed by the continuous colonization of the agricultural matrix by species from the surrounding semi-natural habitats. In cleared homogeneous landscapes dominated by agricultural fields, responses to implementation of AES may also be limited, as few source populations are present to colonize newly created or improved habitats. In contrast, in simple landscapes that contain intermediate levels of semi-natural habitats source populations are still present while the matrix is not continuously colonized, allowing significant responses to implementation of AES. Second, focusing on within-field processes, Kleijn & Sutherland (2003) hypothesized that effectiveness of agri-environmental measures is affected by land-use intensity. Based on competition, niche theory and intermediate disturbance theory, they predicted that effectiveness of agri-environmental measures should decline non-linearly with increasing land-use intensity (e.g rates of agrochemical inputs and agricultural disturbances). As a result, the largest impacts of agri-environmental measures are expected in relatively extensively managed sites, as in intensively farmed areas reduced disturbance rates in sites under agri-environmental management will still be too high for many species to persist. Third, Kleijn *et al.* (2011) suggested that the effects of agri-environmental measures increase with the size of the ecological contrast created by the measures, i.e. the extent to which agri-environmental management improves habitat conditions relative to conventionally managed habitat in terms of resources or sources of mortality. The extent of the induced ecological contrast may be taxon-specific, depends on what specific types of measures are being implemented and, as grasslands are generally less disturbed by agricultural activities than croplands (Herzog *et al.* 2006), may be affected by the farmland type they are implemented in. The response of farmland biodiversity to the created ecological contrast is subsequently expected to be moderated by land-use intensity and landscape context (see further Kleijn *et al.* 2011). For instance, in each landscape type measures creating larger ecological contrasts are expected to be more effective, but the same type of measure is expected to be more effective in simple than in cleared or complex landscapes. Apart from a few studies analysing the moderating effects of landscape context (Batáry *et al.* 2011; Concepción *et al.* 2012), these three hypotheses and the interactions between them are yet to be tested in a systematic manner across the range of available studies.

Here, focusing on pollinating insects, we provide the first comprehensive quantitative review of the factors that potentially moderate the effectiveness of agri-environmental measures. Flower-visiting insects provide vital pollination services to crops and wild plants (Klein *et al.* 2007; Ollerton *et al.* 2011). However, accumulating evidence for declining populations of both wild and managed pollinators in Europe (Biesmeijer *et al.* 2006; Van Swaay *et al.* 2006; Potts *et al.* 2010) has increased the urgency to identify and implement measures that effectively mitigate pollinator loss in agricultural landscapes. Although AES are, with the exception of some UK and Swiss schemes, not specifically targeted at pollinators (Rundlöf & Bommarco 2011), several measures within AES may potentially be beneficial (e.g. Kleijn *et al.* 2006; Haaland *et al.* 2011). For instance, extensification schemes and schemes involving the creation or restoration of non-cropped farmland habitats can, either directly or indirectly, enhance the availability of floral resources, the availability of nesting sites and/or reduce sources of mortality (i.e. pesticides).

Focusing on the most important pollinator taxa, namely bees (Apiformes), hoverflies (Syrphidae) and butterflies and moths (Lepidoptera), we review and synthesize the available evidence to date for effectiveness of agri-environmental measures in promoting pollinators in European agricultural landscapes. Using a meta-analytic approach we examine the factors affecting the effectiveness of agri-environmental measures by addressing the following questions:

1) Are agri-environmental measures more effective in simple than in complex or cleared landscapes?
2) Does the effectiveness of agri-environmental measures decline with increasing land-use intensity?
3) Is measure-induced contrast in resource availability positively related to effectiveness of agri-environmental measures?

MATERIAL AND METHODS

Data collection

We searched the ISI Web of Science, SCOPUS, CAB abstracts, Biological abstracts, AGRICOLA and AGRIS bibliographic databases for studies that addressed the effects of agri-environmental measures on pollinators. Records were included that were published up until October 2011. To minimize potential publication bias associated with the "file drawer problem" (Rosenthal 1979) we also searched for grey literature (McAuley *et al.* 2000) using the Google web search engine and by approaching contacts (nature conservation organisations, scientists) in 26 European countries with a request for relevant reports and unpublished studies available in languages accessible to the authors.

We screened potentially relevant studies for fulfilment of our selection criteria for inclusion. We included only those studies that: (1) Compared the species richness and/or abundance of the focal taxa (Apiformes, Lepidoptera, Syrphidae) between sites with agri-environmental measures and conventionally managed control sites. Measures did not necessarily need to be part of a formal agri-environmental scheme as long as they included environmentally friendly practices that could potentially benefit pollinators. When studies did not use a strict conventional control we used the treatment most closely resembling conventional practice as control (e.g. cropped field margin managed as conservation headland as control for uncropped naturally regenerated field margin treatment (Kells *et al.* 2001)); (2) Reported means, standard deviations (s.d.), standard errors of means (s.e.m.) or confidence intervals (CI) and sample sizes for both treatment and control (in the text, tables, graphs or after requesting the authors) to allow calculation of effect sizes; (3) Included at least four spatial replicates; (4) Were geographically restricted to Europe. Altogether we found 71 studies (including nine grey literature reports and conference proceedings) that matched our selection criteria: 57 studies on pollinator species richness (see Table S1 in Supporting Information) and 69 studies on pollinator abundance (see Table S2).

Ecological factors such as contrasts in plant resource availability may affect the outcome of meta-analyses but are difficult to include because of between-study differences in sampling approach. To explore the importance of a number of hypothesised key ecological factors we incorporated original data collected in the EASY-project into the meta-analysis. Within the framework of this project, data on bee species richness and abundance was collected in 121 paired fields under agri-environmental and conventional management, located in 18 regions in six countries using a standardised sampling protocol (see Kleijn *et al.* 2006 and Batáry *et al.* 2010 for a description of the study design, sampling protocol and types of examined agri-environmental measures). Since no information was available on hoverflies, butterflies and moths, these more in-depth analyses focused on bees only.

Calculation of effect sizes

We used Hegdes' unbiased weighted standardized mean difference (Hedges' *d*) as the metric of effect size in our meta-analysis. Effect sizes and their non-parametric estimates of variance (NP var), which are less constrained by the assumptions of large sample theory (Rosenberg *et al.* 2000), were calculated for each treatment-control pair in the dataset (see Appendix S1). Within individual studies, observations on several of the focal pollinator species groups and observations in different geographical regions or landscape types were considered to be independent and were included as separate cases in the dataset. As a result, several studies contributed more than one entry to the dataset. If a study examined more than one treatment level of a particular type of agri-environmental measure or covered multiple years we selected the treatment level and year with the largest sample size; in case of equal sample sizes we selected the treatment level with the highest expected ecological contrast vis-à-vis conventional management (e.g. in case of sown field margins we used the treatment with the most species rich seed mixture) and used the results of the most recent study year. If individual studies presented separate results for several lower order taxonomic groups (e.g. solitary bees and bumblebees, butterflies and moths) within the focal taxa, for different crops or habitat types, for different types of measures, or for different locations within the studied sites (e.g. centres and edges of treatment and control fields), the results were considered non-independent. To avoid pseudo-replication we calculated effect sizes for each separate comparison in these cases and used the estimated pooled mean within-study effect size in our analyses (see Van Kleunen *et al.* 2010 for a similar approach). However, if individual studies presented results for several categories in categorical meta-analyses, the results were included as separate cases. In these cases the results were grouped among mutually exclusive categories and the potential bias for non-independence is therefore minimized (Lajeunesse 2011).

Meta-analyses

We initially used categorical meta-analyses to test whether agri-environmental measures in general are effective at promoting species richness and abundance of bees, hoverflies and lepidopterans in agro-ecosystems. Next, as grasslands are generally less disturbed by agricultural activities than croplands (Herzog *et al.* 2006), we examined whether effectiveness of agri-environmental measures is affected by the farmland type in which the measures are being implemented (croplands versus grasslands). Cropland (arable fields and field margins) mainly consisted of cereal fields, but also included maize, root crops, beans, oilseed rape and vineyards. Grassland consisted of permanent grasslands for grazing or hay making. Because effect sizes differed significantly between farmland types (see Results section), subsequent analyses of factors affecting effectiveness of agri-environmental measures were, sample size allowing, performed separately for studies in croplands and grasslands.

To address the question whether landscape context influences effectiveness of agri-environmental measures we analysed whether mean effect sizes differed across categories of cleared, simple and complex landscapes. Following Tscharntke *et al.* (2005), studies were classified as having been conducted in structurally cleared, simple or complex landscapes if the study landscapes (1000m radius around study sites) respectively contained less than 1%, 1 to 20%, or more than 20% (semi-)natural habitat. Classifications of study landscapes were based on available landscape data in the studies (presented in the papers or provided by the authors) or on visual assessment of study landscapes using Google Earth software. We were able to classify study landscapes of 23 studies (50 cases) on pollinator species richness and 24 studies (52 cases) on abundance.

As the ecological contrast that is induced by agri-environmental measures may differ with the type of measure being implemented, we used categorical meta-analyses to assess to what extent different types of measures differ in effectiveness. Based on the nature of the different measures covered by the studies in the species richness and abundance datasets, we divided the studies into four categories of measure-types: (1) sown flower strips (uncropped farmland habitats such as field margins, set-aside or other patches sown with insect-pollinated herbs), (2) extensive grasslands (pasture or meadow under an extensification scheme), (3) organic farming, (4) grass-sown or naturally regenerated uncropped farmland habitats such as field margins or set-aside. Furthermore, for studies on sown flower strips we analysed the relationship between effectiveness and the number of flower species that were sown, using continuous meta-analyses (meta-regressions).

We used data on nitrogen input (annual nitrogen input per site in kg N ha^{-1} yr^{-1}) collected in the EASY-project to analyse the relationship between local land-use intensity and effectiveness of agri-environmental measures. 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; Kleijn *et al.* 2009). We therefore used the mean nitrogen input in control fields in each of the 18 regions as an explanatory variable in continuous meta-analyses.

Data from the EASY-project were also used in meta-regressions to analyse the relationship between effectiveness of agri-environmental measures and the measure-induced contrast in habitat quality. The standardized protocol for sampling forb cover and species richness employed in the EASY-project allowed us to test whether the mean contrasts in forb species richness and forb cover between fields with agri-environmental measures and control fields affected the magnitude of effect sizes. In addition, we analysed whether effectiveness of agri-environmental measures was influenced by the mean forb species richness and forb cover of control fields (as proxy for the landscape-wide availability of flower resources).

All meta-analyses were performed using MetaWin version 2.1 (Rosenberg *et al.* 2000). We used categorical and continuous random effects models (mixed effects models) to address our research questions. Such models assume that differences among studies result from sampling error and true random variation due to biological or environmental differences between organisms and studies, and are therefore the preferred models for ecological data (Gurevitch & Hedges 1999). In the categorical comparisons we tested whether mean effect sizes differed between subgroups by assessing the significance of the between-group heterogeneity (Q_B), which describes the variation in effect sizes that can be attributed to differences between categories. Subgroups with less than four cases were excluded from categorical analyses. In the continuous meta-analyses, we used inverse-variance-weighted least-squares regressions to test whether variation in effect sizes could be explained by the independent continuous variables. For significant regressions we calculated r^2 values by dividing Q_M (heterogeneity explained by the model) by Q_T (total heterogeneity) (Myers & Harms 2009).

We visually inspected normal quantile plots to determine if the datasets were normally distributed (Wang & Bushman 1998). When effect sizes were approximately normally distributed we calculated parametric 95% confidence intervals (CI's) around mean effect sizes and used parametric significance tests. In case of non-normally distributed data we calculated bias-corrected bootstrap 95% CI's (except for datasets with number of studies (k) < 10 because of bias due to resampling from the same small set of values (Bancroft *et al.* 2007)) and tested for significance using randomization tests with 64,999 iterations (Adams *et al.* 1997). A mean effect size was considered significant when its 95% CI did not contain zero.

Publication bias in all datasets (except the datasets used in the EASY-project meta-regressions) was assessed by inspecting normal quantile plots and calculating Rosenthal's fail-safe numbers (Rosenthal 1979). Normal quantile plots did not indicate publication bias in any of the datasets and calculated failsafe numbers were robust in each of the analyses.

RESULTS

Overall, agri-environmental measures had significant positive effects on species richness (mean effect size (d_+) = 0.98, 95% CI = 0.79 to 1.17, k = 102) and abundance ($d_+ = 0.88$, 95% CI = 0.72 to 1.04, k = 121) of pollinators in agroecosystems. The magnitude of the overall effects did not differ between bees, lepidopterans and hoverflies (mixed effects model using pollinator taxa as factor; species richness $Q_B = 1.13$, $P_{random} = 0.59$; abundance $Q_B = 2.79$, $P = 0.25$).

The farming system in which agri-environmental measures were implemented clearly affected the effectiveness of the measures. Pollinator species richness was enhanced by measures in croplands (d_+ = 1.37, 95% CI = 1.03 to 1.51, k = 60) as well as grasslands (d_+ = 0.56, 95% CI = 0.28 to 0.83, k = 43), but the magnitude of the observed effect was significantly larger in croplands than in grasslands (Q_B = 15.61, $P < 0.001$). A similar pattern was observed for pollinator abundance (cropland d_+ = 1.03, 95% CI = 0.83 to 1.23, k = 78; grassland d_+ = 0.49, 95% CI = 0.23 to 0.75, k = 46; Q_B = 10.84, P = 0.001).

Landscape context

Effectiveness of agri-environmental measures in promoting pollinator species richness and abundance was moderated by landscape context (species richness Q_B = 7.51, P = 0.023; abundance Q_B = 6.49, P = 0.039). Effects were largest in simple landscapes, smaller in complex landscapes and non-significant in cleared landscapes (Fig. 1). Separate analyses of the effects of landscape context on effectiveness of measures implemented in croplands and grasslands revealed that the overall pattern of landscape-moderated effectiveness of agri-environmental measures was reflected in both cropland and grassland systems (Fig. S1). However, sample sizes were low in these separate analyses and between-group heterogeneity statistics were not significant (cropland: species richness Q_B = 2.10, P = 0.15; abundance Q_B = 2.91, P = 0.23; grassland: species richness Q_B = 4.34, P = 0.11; abundance Q_B = 2.67, P = 0.26).

Figure 1. The effects of agri-environmental measures on pollinator species richness and abundance, depending on landscape context. Structurally cleared landscapes: < 1% semi-natural habitat; simple landscapes: 1 – 20% semi-natural habitat; complex landscapes: > 20% semi-natural habitat. Indicated are mean effect sizes (Hedges'*d*) ± 95% CI. A mean effect size is considered significant when its CI does not include zero. Numbers indicate sample sizes.

Types of measures

The impact of agri-environmental measures on pollinators varied with the type of measures that were implemented. In croplands, all types of agri-environmental measures effectively enhanced species richness (Fig. 2a) and abundance (Fig. 2c) of pollinators. The magnitude of the effectiveness for species richness did not differ among the measure-types (Q_B = 1.66, P_{random} = 0.51). However, measure-types differed in their effects on abundance, with the largest mean effect size observed for sown flower strips and the smallest mean effect size for organic farming (Q_B = 8.02, P = 0.018). In grasslands different types of measures varied in their effectiveness for both species richness (Q_B = 34.73, $P < 0.001$) and abundance (Q_B = 24.01, $P < 0.001$) and organic farming did not significantly enhance pollinators at all. For both species richness and abundance, effect sizes were largest for sown flower strips, smaller for extensive grasslands and non-significant for organic farming (Fig. 2b, d).

Regarding the flower strips, meta-regressions showed that the number of flower species that were sown was positively related with effect size for pollinator abundance (Q_M =

7.50, k = 30, $P = 0.006$, $r^2 = 0.18$; Fig. 3a) but not species richness ($Q_M = 2.43$, k = 24, $P = 0.12$; Fig. 3b). However, when only the obligate pollen feeding bees were considered, the number of sown flower species in strips was significantly related with the effectiveness of flower strips in increasing both species richness ($Q_M = 7.43$, k = 9, $P = 0.006$, $r^2 = 0.53$; Fig. 3a) and abundance ($Q_M = 11.01$, k = 12, $P < 0.001$, $r^2 = 0.50$; Fig. 3b) of bees.

Land-use intensity

Mean nitrogen input in control fields ranged from 25 to 262 kg N ha^{-1} yr^{-1} in croplands and from 0 to 285 kg N ha^{-1} yr^{-1} in grasslands across the study regions in the EASY-project. Nitrogen input did not influence the effects of agri-environmental measures on bee species richness and abundance (Fig. S2) in either cropland (species richness $Q_M = 0.36$, k = 8, $P = 0.55$; abundance $Q_M = 1.52$, k = 8, $P = 0.28$) or grassland (species richness $Q_M = 0.02$, k = 9, $P = 0.89$; abundance $Q_M = 0.10$, k = 9, $P = 0.75$).

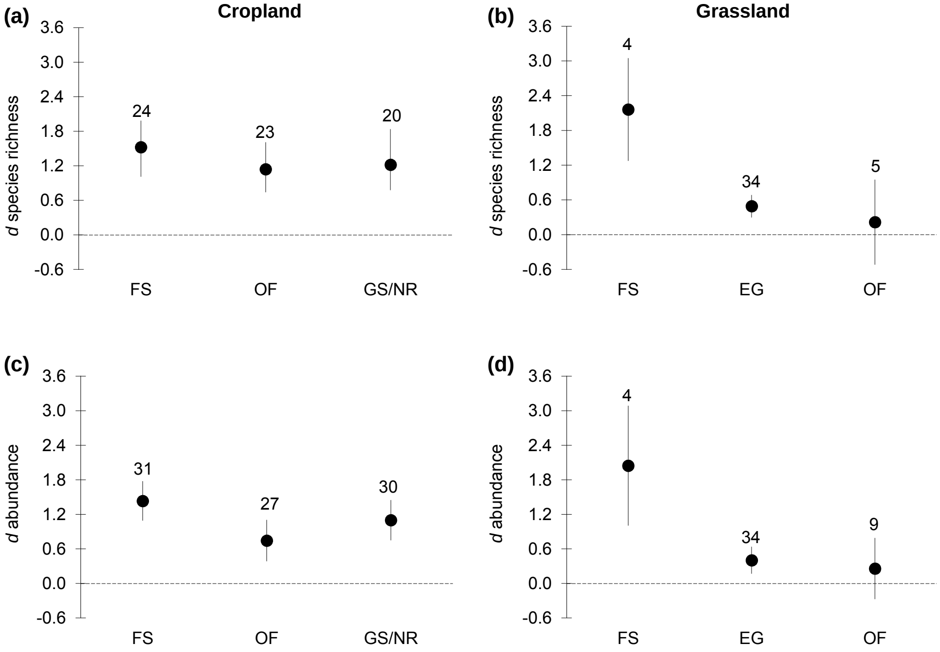

Figure 2. Effects of different types of agri-environmental measures on species richness (top) and abundance (bottom) of pollinators in croplands (left) and grasslands (right). Indicated are mean effect sizes (Hedges'*d*) ± 95% bias corrected bootstrap CI (a) or parametric 95% CI (b, c, d). Numbers indicate sample sizes. FS: sown flower strip; OF: organic farming; GS/NR: grass-sown or naturally regenerated field margin or set-aside; EG: extensive grassland.

Ecological contrast

In croplands, the impact of agri-environmental measures on species richness of bees increased significantly with the measure-induced contrast in forb species richness ($Q_M = 9.63$, k = 8, $P = 0.002$, $r^2 = 0.62$; Fig. 4a) and the induced contrast in forb cover ($Q_M = 8.92$, $P = 0.003$, $r^2 = 0.58$; Fig. 4 b). Effects of agri-environmental measures were negatively related with forb species richness ($Q_M = 4.26$, $P = 0.039$, $r^2 = 0.41$; Fig. 4c) and forb cover ($Q_M = 7.76$, $P = 0.005$, $r^2 = 0.56$; Fig. 4d) in control fields. In contrast, in grasslands no significant relations with the contrast in forb species richness (Q_M = 0.62, k = 9, P = 0.43; Fig. 4a), the contrast in forb cover (Q_M = 0.05, P = 0.82; Fig. 4b), the species richness of forbs in control fields (Q_M = 0.64, P = 0.42; Fig. 4c) and the forb cover in control fields (Q_M = 2.86, P = 0.09; Fig. 4d) were found. Similar patterns were observed in the analyses of effects on bee abundance, but only the contrast in forb species richness and the forb species richness in control fields in croplands were respectively significantly positively ((Q_M = 5.69, P = 0.017, r^2 = 0.53) and negatively (Q_M = 5.12, P = 0.024, r^2 = 0.48) related with the impact of agri-environmental measures on bee abundance (Table S3).

DISCUSSION

Agri-environmental measures in Europe generally enhance species richness and abundance of the most important groups of pollinators, but the strength of the response is primarily driven by landscape context and the ecological contrast induced by agri-environmental measures. Measures were more effective at enhancing pollinators in structurally simple than in cleared or complex landscapes and effectiveness of measures increased with increasing induced contrast in floral resource availability. The extent to which measures create an ecological contrast appears to differ between farmland types. In croplands each type of measure enhanced pollinator species richness and abundance, and effectiveness increased with increasing contrast in resource availability, whereas in grasslands no clear relationships were observed between contrast in resource availability and effectiveness of agri-environmental measures. The largest ecological contrasts and pollinator responses were observed in intensively farmed arable landscapes where conventional farming has decimated floral resource availability.

The observed differential effects of farmland type on effectiveness of agri-environmental measures may be explained by differences in disturbance regimes. Compared to croplands, grasslands are usually less disturbed by agricultural management (Herzog *et al.* 2006), resulting in relatively smaller habitat-matrix differences in grasslands than in croplands – even intensively managed grasslands can provide suitable nesting sites and foraging resources (e.g. Fabaceae, Asteraceae) for pollinators (Kohler *et al.* 2007; Marini *et al.* 2012). Furthermore, the closed perennial vegetation in grasslands is not easily colonized by new plant species (unless the soil is cultivated), thereby limiting the response of grassland plant communities to introduction of measures. In contrast, the deep tillage, agro-chemical application and complete vegetation removal associated with cropland management creates a relatively hostile matrix with little foraging (with the exception of mass-flowering crops (Le Féon *et al.* 2010)) and nesting opportunities. Additionally, in the frequently tilled soils associated with croplands, plants may readily respond to reductions in management intensity. In such systems, even relatively simple measures such as conservation headlands can significantly enhance flower resources for pollinators (Pywell *et al.* 2005).

Landscape complexity, measured as the proportion of semi-natural habitat in the landscape, affected the magnitude of the effects of agri-environmental measures. In line with the intermediate landscape-complexity hypothesis proposed by Tscharntke *et al.* (2005) we found that effectiveness of agri-environmental measures in promoting species richness and abundance of pollinators was highest in structurally simple landscapes that have intermediate levels of semi-natural habitat (Fig. 1). Our study complements findings of Batáry *et al.* (2011) and Concepción *et al.* (2012) in providing results on the relatively under-studied cleared landscapes (Tscharntke *et al.* 2012). However, we must note that all studies performed in cleared landscapes were conducted in The Netherlands, suggesting geographical bias. Yet, The Netherlands is one of the most intensively farmed countries in Europe (Herzog *et al.*

2006) and contains relatively large proportions of cleared landscapes, so it is not surprising that studies performed in cleared landscapes originated from this country. In addition, our overall dataset of 71 studies covered several European countries, but studies from the UK (26), Germany (10) and Sweden (10) were overrepresented in the dataset, resulting in a geographical bias towards North-Western European countries. Our results should therefore be interpreted bearing this geographical bias in mind (Tryjanowski *et al.* 2011).

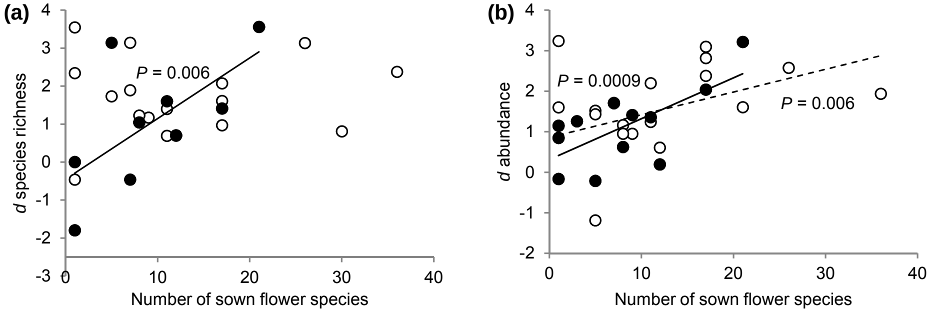

Figure 3. Relationship between the number of forb species sown in flower strips and effects of flower strips on species richness (a) and abundance (b) of all pollinators (all circles, dashed regression lines) and bees separately (filled circles, solid regression lines). Regression lines and *P*-values are shown for significant meta-regressions.

We found no support for the hypothesis that the effectiveness of agri-environmental measures declines with increasing land-use intensity (Kleijn & Sutherland 2003). The basis for this hypothesis is that biodiversity declines exponentially with increasing land-use intensity which would result in more pronounced effects of measures on biodiversity in extensively farmed areas than in more intensively farmed areas. Kleijn *et al.* (2009) indeed found exponentially declining plant species richness with increasing land-use intensity. However, this relationship seems to vary between species groups (Gabriel *et al.* 2013) and bees may actually decline linearly with increasing land-use intensity (Le Féon *et al.* 2010), suggesting that an equal reduction in land use intensity would result in an equal increase in bee species richness and abundance in extensively as well as intensively farmed areas.

We found significant differences between measure-types in their effectiveness to enhance pollinator species richness (only in grasslands) and abundance (in both croplands and grasslands). In croplands as well as grasslands, mean effect sizes were largest for sown flower strips and smallest (or non-significant in grasslands) for organic farming (Fig. 2). The observed differences in effect sizes between flower strips and other measures may have partly been driven by the scale of the study. Flower strips are mainly implemented at the plot or field scale whereas measures such as organic farming are implemented at the farm scale. Part of the pronounced effects of flower strips may therefore be explained by an attraction process associated with the small scale of implementation (Veddeler *et al.* 2006). On the other hand, the effectiveness of the flower strips increased with the number of sown flower species (Fig. 3) and the consistently large effect sizes of flower strips reflect the more targeted way in which these habitats are created, i.e. through direct enhancement of floral resources (Pywell *et al.* 2005). In general, the abundance and diversity of floral resources are key factors limiting pollinator population sizes (Müller *et al.* 2006; Roulston & Goodell 2011) and the effects of the different measure-types on pollinators therefore appear to be predominantly mediated by direct or indirect enhancement of flower resource availability (Gabriel & Tscharntke 2007; Kohler *et al.* 2007; Aviron *et al.* 2011). This suggests that, for pollinators, the ecological contrast in floral resources created by agri-environmental measures seems to be a key driver of the effectiveness of measures (Fig. 4). Interestingly and in line with Carvell *et al.* (2011), we found a negative relationship between the effectiveness of agri-environmental measures and flower resource availability in conventionally managed fields. This implies that the ecological contrast induced by agri-environmental measures does not only depend on the resource availability associated with a particular measure, but also on the landscape-wide availability of alternative resources. Obviously, it is more difficult for agri-environmental measures to create a contrast in resource availability in resource-rich than in resource-poor landscapes. However, besides enhancing floral resources, the different measure-types may benefit pollinators by creating ecological contrasts in terms of nesting sites or incidental risk factors (sensu Roulston & Goodell 2011) such as exposure to pesticides.

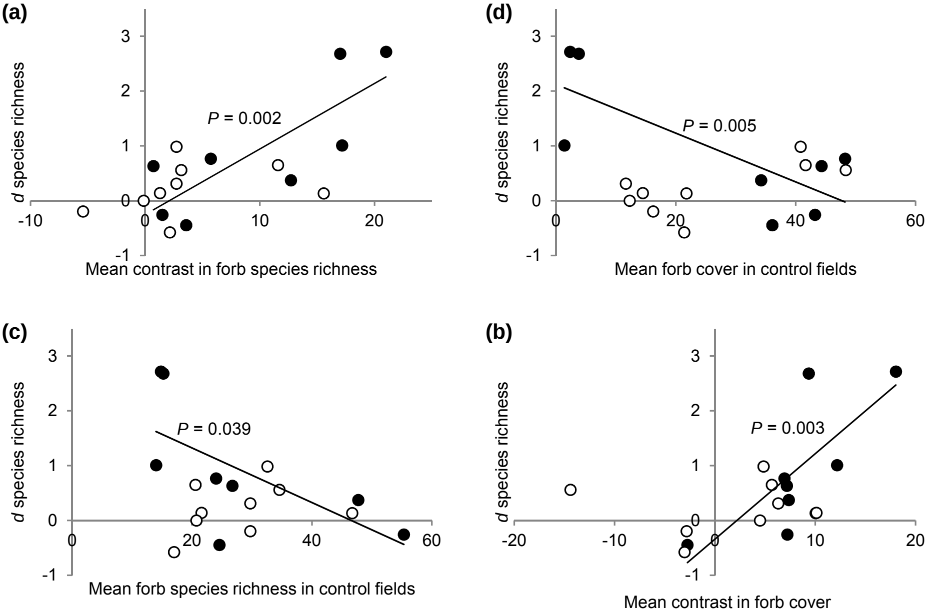

Figure 4. Effects of measure-induced contrasts in resource availability (a, b) and the availability of resources in control fields (c, d) on effectiveness of agri-environmental measures in promoting bee species richness in croplands (filled circles, solid regression lines) and grasslands (open circles). Regression lines and *P*-values are shown for significant meta-regressions.

Our results show that by improving resource availability agri-environmental measures generally promote pollinators in agricultural landscapes. Given that resource availability most likely regulates pollinator populations (Roulston & Goodell 2011), this suggests that agri-environmental measures probably have positive effects on populations. However, nearly all studies in our dataset measured species richness and abundance of foraging pollinators and studies measuring population responses of pollinators were scarce. We therefore have no concrete evidence that the observed patterns reflect population responses or just reflect behavioural spatio-temporal concentration and dilution processes (i.e. creating temporary localized sinks, Kleijn *et al.* 2011). So, although improvements in resource availability induced by agri-environmental measures may be expected to lead to population-level responses (Müller *et al.* 2006), the species richness and abundance data used in the present study do not merit unambiguous conclusions about population-level effects.

CONCLUSION

Insight into the ecological factors that explain the success or failure of agri-environmental measures is essential if we want AES to contribute to the halting or reversing of biodiversity loss on farmland. Our study shows that agri-environmental measures generally enhance local pollinator species richness and abundance in agroecosystems, and are most effective when implemented in structurally simple, resource-poor landscapes dominated by arable fields where they readily create large ecological contrasts. However, these landscapes mainly support common generalist species with good dispersal capacities (Bommarco *et al.* 2010; Ekroos *et al.* 2010) that may readily respond to habitat improvement induced by agri-environmental measures (Kleijn *et al.* 2006; Aviron *et al.* 2011), but are of relatively little interest from a biodiversity conservation perspective. Yet, the common generalist pollinator species are most likely the species that contribute most to the pollination of crops and many cultivated forbs (Vásquez *et al.* 2005). So, from the perspective of ecosystem service delivery the implementation of AES should preferentially be directed at these relatively simple, resource-poor landscapes. In contrast, if the objective is to preserve intrinsic values of biodiversity, agri-environmental management should target more complex landscapes that support species rich pollinator communities (Billeter *et al.* 2008) and are likely to support more rare, specialist pollinator species. Ultimately, the design and implementation of AES should be governed by clear conservation or ecosystem service targets, although each does not necessarily exclude the other. Evaluation schemes of AES targeted at delivery of pollination services need to include estimates of increased yields from improved pollination, while those targeted at biodiversity conservation need to include measurement of population-level responses of pollinators, including rare species.

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SUPPORTING INFORMATION

Appendix S1. Methods to calculate Hedges *d* effect size and associated non-parametric estimate of sampling variance.

Figure S1. Landscape dependent effects of agri-environmental measures on pollinator species richness and abundance in croplands and grasslands.

Figure S2. Relationship between land-use intensity and effects of agri-environmental measures on bee species richness and abundance.

Table S1 Summary of data used in the pollinator species richness analyses.

Table S2 Summary of data used in the pollinator abundance analyses.

Table S3. Regression coefficients and heterogeneity statistics for the continuous meta-analyses of the relationship between (contrasts) in resource availability and effects of AES on pollinator abundance in croplands and grasslands.

Appendix S1 Calculation of effect size and non-parametric variance

An effect size (Hedges *d*) was calculated for each treatment-control pair in the pollinator species richness and abundance datasets. Hedges d is not biased by small sample sizes and unequal sampling variances and can be applied to datasets that contain zeros (Rosenberg *et al.* 2000). Using the mean species richness and abundance of pollinators per spatial replicate in agri-environmentally managed sites (treatment mean X_T) and conventionally managed sites (control mean X_C), the standard deviations for the treatment (S_T) and control (S_C), and sample sizes (the number of spatial replicates, e.g. sites or fields) for the treatment (N_T) and control (N_C), Hedges' *d* was calculated as (Hedges & Olkin 1985):

$$d = \frac{(\bar{X}_T - \bar{X}_C)}{S_{pooled}} J$$

where the pooled standard deviation S_{pooled} is:

$$S_{pooled} = \sqrt{\frac{(N_T - 1)(S_T)^2 + (N_C - 1)(S_C)^2}{N_T + N_C - 2}}$$

and where the correction term for small sample size *J* is:

$$J = 1 - \frac{3}{4(N_C + N_T - 2) - 1}$$

The species richness and abundance data reported in the primary studies in our datasets may violate the assumption of Hedges' d that observations in the experimental and control groups are normally distributed for each study. We therefore calculated non-parametric estimates of the sampling variance for the effect size in each study, following Hedges & Olkin (1985):

$$NP\ var = \frac{(N_C + N_T)}{N_C N_T}$$

Non-parametric estimates of sampling variance are less constrained by the assumptions of large sample theory (Hedges & Olkin 1985). Calculation of these estimates only incorporates the sample sizes of the treatment and control groups rather than the effect size, while still counting larger studies more heavily than small ones (Adams *et al.* 1997).

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Figure S1. Landscape dependent effects of agri-environmental measures on pollinator species richness and abundance in croplands (a) and grasslands (b). Structurally cleared landscapes: < 1% semi-natural habitat; simple landscapes: 1 – 20% semi-natural habitat; complex landscapes: > 20% semi-natural habitat. Indicated are mean effect sizes (Hedges'*d*) ± 95% CI. Numbers indicate sample sizes. Note: in croplands too few studies were available to include cleared landscapes in the species richness analysis.

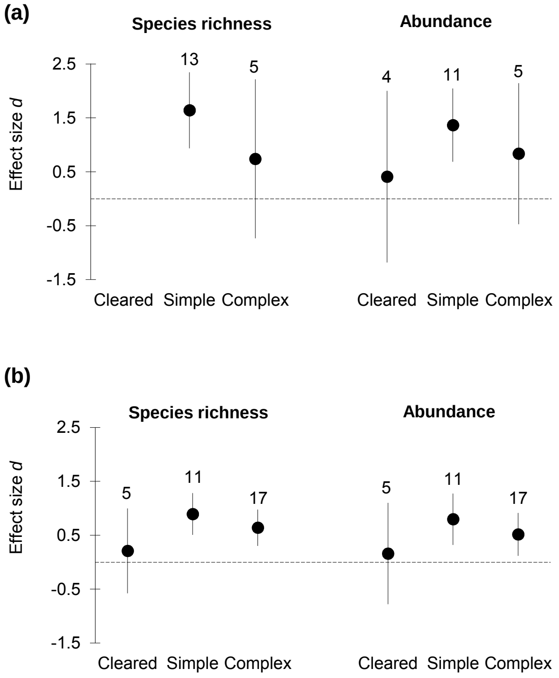

Figure S2. Relationship between land-use intensity, measured as annual nitrogen input, and effects of agri-environmental measures on bee species richness (a) and abundance (b) in croplands (filled circles) and grasslands (open circles).

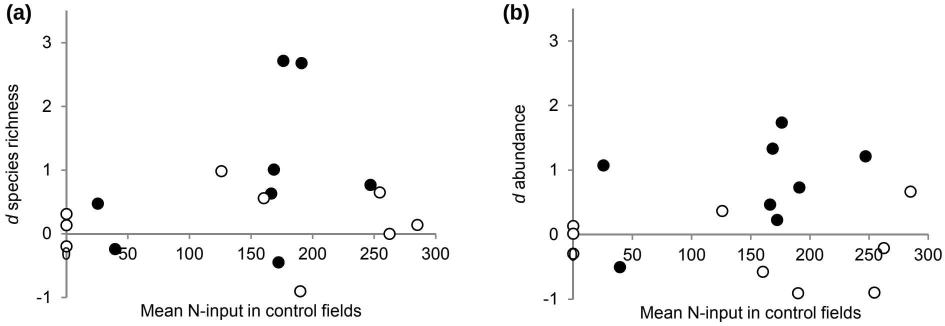

Table S1. Summary of data used in the pollinator species richness analyses. References for grey literature are shown underlined; references for the EASY data are shown in bold.

Study no.	**Source**	**Country**	**Region / landscape**	**Order / family**	**Species / group**	**Farmland type**	**Measure-type**	**Hedges' *d***	**NP var (*d*)**
1	Alanen *et al.* 2011	Finland	-	Apiformes	Bumblebees	Cropland	Sown flower strips	0.704	0.500
1	Alanen *et al.* 2011	Finland	-	Lepidoptera	Butterflies and diurnal moths	Cropland	Sown flower strips	0.694	0.500
2	Albrecht *et al.* 2007a	Switzerland	-	Apiformes	Bees	Grassland	Extensive grassland	1.615	0.154
2	Albrecht *et al.* 2007a	Switzerland	-	Lepidoptera	Butterflies	Grassland	Extensive grassland	0.517	0.154
2	Albrecht *et al.* 2007a	Switzerland	-	Syrphidae	Hoverflies	Grassland	Extensive grassland	1.279	0.154
3	Albrecht *et al.* 2007b	Switzerland	-	Apiformes	Solitary bees	Grassland	Extensive grassland	0.456	0.154
4	Albrecht *et al.* 2010	Switzerland	-	Apiformes	Bees	Grassland	Extensive grassland	1.271	0.083
5	Aviron *et al.* 2009	Switzerland	Grassland and mixed arable-grassland region	Lepidoptera	Butterflies	Grassland	Extensive grassland	0.149	0.008
5	Aviron *et al.* 2009	Switzerland	Arable region	Lepidoptera	Butterflies	Cropland	Sown flower strips	0.811	0.027
6	Aviron *et al.* 2010	Switzerland	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	2.375	0.088
7	**Batary *et al.* 2010**	Hungary	Alkali	Apiformes	Bees	Grassland	Extensive grassland	0.312	0.286
7	**Batary *et al.* 2010**	Hungary	Meadow	Apiformes	Bees	Grassland	Extensive grassland	0.134	0.286
7	**Batary *et al.* 2010**	Hungary	Heves	Apiformes	Bees	Grassland	Extensive grassland	-0.196	0.286
8	Blake *et al.* 2011a	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	1.170	0.333
9	Brittain *et al.* 2010	Italy	-	Apiformes	Solitary bees	Cropland	Organic farming	-0.113	0.333

9	Brittain *et al.* 2010	Italy	-	Lepidoptera	Butterflies	Cropland	Organic farming	0.340	0.333
10	Buys *et al.* 1997	The Netherlands	-	Apiformes	Bumblebees and honeybees	Cropland	Sown flower strips	1.599	0.041
10	Buys *et al.* 1997	The Netherlands	-	Apiformes	Bumblebees and honeybees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.385	0.077
10	Buys *et al.* 1997	The Netherlands	-	Apiformes	Bumblebees and honeybees	Cropland	Overall measure-type effect size	1.525	0.059
10	Buys *et al.* 1997	The Netherlands	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	1.399	0.041
10	Buys *et al.* 1997	The Netherlands	-	Lepidoptera	Butterflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.482	0.077
10	Buys *et al.* 1997	The Netherlands	-	Lepidoptera	Butterflies	Cropland	Overall measure-type effect size	1.428	0.059
10	Buys *et al.* 1997	The Netherlands	-	Syrphidae	Hoverflies	Cropland	Sown flower strips	0.693	0.077
10	Buys *et al.* 1997	The Netherlands	-	Syrphidae	Hoverflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.303	0.142
10	Buys *et al.* 1997	The Netherlands	-	Syrphidae	Hoverflies	Cropland	Overall measure-type effect size	0.556	0.110
11	Carvell *et al.* 2007	United Kingdom	-	Apiformes	Bumblebees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.845	0.333
11	Carvell *et al.* 2007	United Kingdom	-	Apiformes	Bumblebees	Cropland	Sown flower strips	3.560	0.333
11	Carvell *et al.* 2007	United Kingdom	-	Apiformes	Bumblebees	Cropland	Overall measure-type effect size	2.203	0.333
12	**Concepción *et al.* 2008**	Spain	Retuerta del Bullaque	Apiformes	Bees	Cropland	Other	-0.238	0.286
12	**Concepción *et al.* 2008**	Spain	Huecas	Apiformes	Bees	Cropland	Other	0.373	0.286
13	De Snoo *et al.* 1998	The Netherlands	-	Lepidoptera	Butterflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.318	0.238

14	Dover *et al*. 2000	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Other	3.888	0.194
15	Ekroos *et al*. 2008	Finland	-	Apiformes	Bumblebees	Cropland	Organic farming	0.539	0.092
15	Ekroos *et al*. 2008	Finland	-	Lepidoptera	Diurnal macrolepidoptera	Cropland	Organic farming	-0.040	0.092
16	Feber *et al*. 1996	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	1.610	0.250
16	Feber *et al*. 1996	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.600	0.250
16	Feber *et al*. 1996	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Overall measure-type effect size	1.105	0.250
17	Feber *et al*. 2007	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Organic farming	0.650	0.200
18	Fuentes-Montemayor *et al*. 2011	United Kingdom	-	Lepidoptera	Macromoths	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.141	0.125
18	Fuentes-Montemayor *et al*. 2011	United Kingdom	-	Lepidoptera	Macromoths	Cropland and grassland	Other	0.000	0.154
18	Fuentes-Montemayor *et al*. 2011	United Kingdom	-	Lepidoptera	Macromoths	Cropland and grassland	Sown flower strips	0.414	0.125
18	Fuentes-Montemayor *et al*. 2011	United Kingdom	-	Lepidoptera	Macromoths	Cropland and grassland	Overall measure-type effect size	0.183	0.132
19	Gathmann *et al*. 1994	Germany	-	Apiformes	Solitary bees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.000	0.500
19	Gathmann *et al*. 1994	Germany	-	Apiformes	Solitary bees	Cropland	Sown flower strips	0.000	0.500
19	Gathmann *et al*. 1994	Germany	-	Apiformes	Solitary bees	Cropland	Overall measure-type effect size	0.000	0.500
20	Haenke *et al*. 2009	Germany	-	Syrphidae	Hoverflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.791	0.286

20	Haenke *et al.* 2009	Germany	-	Syrphidae	Hoverflies	Cropland	Sown flower strips	3.135	0.286
20	Haenke *et al.* 2009	Germany	-	Syrphidae	Hoverflies	Cropland	Overall measure-type effect size	2.463	0.286
21	Hodgson *et al.* 2010	United Kingdom	Coldspot	Lepidoptera	Butterflies	Cropland	Organic farming	0.051	0.250
21	Hodgson *et al.* 2010	United Kingdom	Coldspot	Lepidoptera	Butterflies	Grassland	Organic farming	-0.094	0.250
21	Hodgson *et al.* 2010	United Kingdom	Coldspot	Lepidoptera	Butterflies	Overall farmland type effect size	Organic farming	-0.021	0.250
21	Hodgson *et al.* 2010	United Kingdom	Hotspot	Lepidoptera	Butterflies	Cropland	Organic farming	0.000	0.250
21	Hodgson *et al.* 2010	United Kingdom	Hotspot	Lepidoptera	Butterflies	Grassland	Organic farming	0.408	0.268
21	Hodgson *et al.* 2010	United Kingdom	Hotspot	Lepidoptera	Butterflies	Overall farmland type effect size	Organic farming	0.197	0.259
22	**Holzschuh *et al.* 2007**	Germany	Göttingen-simple	Apiformes	Bees	Cropland	Organic farming	2.502	0.333
22	**Holzschuh *et al.* 2007**	Germany	Göttingen-complex	Apiformes	Bees	Cropland	Organic farming	1.714	0.333
22	**Holzschuh *et al.* 2007**	Germany	Soest	Apiformes	Bees	Cropland	Organic farming	1.009	0.333
22	**Holzschuh *et al.* 2007**	Germany	Marburg	Apiformes	Bees	Cropland	Organic farming	2.715	0.400
23	Holzschuh *et al.* 2010	Germany	-	Apiformes	Solitary bees	Cropland	Organic farming	0.354	0.087
24	Hopkins and Feber 1997	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	1.730	0.400
25	Jonason *et al.* 2011	Sweden	-	Lepidoptera	Butterflies	Cropland	Organic farming	0.848	0.075
26	Kleijn *et al.* 1999	The Netherlands	-	Apiformes	Bees	Grassland	Extensive grassland	-0.086	0.286
26	Kleijn *et al.* 1999	The Netherlands	-	Lepidoptera	Butterflies	Grassland	Extensive grassland	-0.269	0.286

26	Kleijn *et al.* 1999	The Netherlands	-	Syrphidae	Hoverflies	Grassland	Extensive grassland	0.171	0.286
27	Kleijn *et al.* 2004	The Netherlands	Clay	Apiformes	Bees	Grassland	Extensive grassland	0.867	0.182
27	Kleijn *et al.* 2004	The Netherlands	Peat	Apiformes	Bees	Grassland	Extensive grassland	0.740	0.125
27	Kleijn *et al.* 2004	The Netherlands	Sand	Apiformes	Bees	Grassland	Extensive grassland	0.957	0.200
27	Kleijn *et al.* 2004	The Netherlands	Clay	Syrphidae	Hoverflies	Grassland	Extensive grassland	0.378	0.182
27	Kleijn *et al.* 2004	The Netherlands	Peat	Syrphidae	Hoverflies	Grassland	Extensive grassland	0.697	0.125
27	Kleijn *et al.* 2004	The Netherlands	Sand	Syrphidae	Hoverflies	Grassland	Extensive grassland	0.361	0.200
28	**Kleijn *et al.* 2006**	The Netherlands	Eempolder	Apiformes	Bees	Grassland	Extensive grassland	-0.577	0.286
28	**Kleijn *et al.* 2006**	The Netherlands	Utrechtse en Hollandse Venen	Apiformes	Bees	Grassland	Extensive grassland	0.141	0.286
28	**Kleijn *et al.* 2006**	The Netherlands	Alblasserwaard and Vijfheerenlanden	Apiformes	Bees	Grassland	Extensive grassland	0.000	0.286
29	**Knop *et al.* 2006**	Switzerland	Ruswill	Apiformes	Bees	Grassland	Extensive grassland	0.650	0.286
29	**Knop *et al.* 2006**	Switzerland	Bauma	Apiformes	Bees	Grassland	Extensive grassland	0.560	0.286
29	**Knop *et al.* 2006**	Switzerland	Flühli	Apiformes	Bees	Grassland	Extensive grassland	0.985	0.286
30	Kohler *et al.* 2008	The Netherlands	-	Apiformes	Bees	Grassland	Sown flower strips	1.411	0.220
30	Kohler *et al.* 2008	The Netherlands	-	Syrphidae	Hoverflies	Grassland	Sown flower strips	2.071	0.220
31	Kovács-Hostyánszki *et al.* 2011a	Hungary	-	Apiformes	Bees	Cropland	Other	1.233	0.250
32	Kovács-Hostyánszki *et al.*	Hungary	-	Apiformes	Bees	Cropland	Sown flower strips	-1.796	0.229

	2011b								
32	Kovács-Hostyánszki *et al.* 2011b	Hungary	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	3.547	0.229
33	Krauss *et al.* 2011	Germany	-	Apiformes	Bumblebees	Cropland	Organic farming	2.624	0.133
33	Krauss *et al.* 2011	Germany	-	Lepidoptera	Butterflies	Cropland	Organic farming	1.117	0.133
33	Krauss *et al.* 2011	Germany	-	Syrphidae	Hoverflies	Cropland	Organic farming	2.241	0.133
34	Kruess and Tscharntke 2002	Germany	-	Apiformes	Bees	Grassland	Extensive grassland	1.218	0.367
34	Kruess and Tscharntke 2002	Germany	-	Lepidoptera	Butterflies and Burnet moths	Grassland	Extensive grassland	1.473	0.333
35	Kuussaari *et al.* 2011	Finland	-	Apiformes	Bumblebees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.780	0.500
35	Kuussaari *et al.* 2011	Finland	-	Lepidoptera	Butterflies and diurnal moths	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.439	0.500
36	Kvarnbäck 2009	Sweden	-	Apiformes	Bumblebees	Cropland	Sown flower strips	1.046	0.400
36	Kvarnbäck 2009	Sweden	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	1.225	0.400
37	Littlewood *et al.* 2008	United Kingdom	-	Lepidoptera	Nocturnal moths	Grassland	Extensive grassland	0.255	0.333
38	Mand *et al.* 2001	Estonia	-	Apiformes	Bumblebees	Cropland and grassland	Organic farming	0.821	0.167
39	**Marshall *et al.* 2004**	United Kingdom	Areas with small field sizes	Apiformes	Bees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	-0.447	0.286
39	**Marshall *et al.* 2004**	United Kingdom	Areas with intermediate field sizes	Apiformes	Bees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.767	0.286
39	**Marshall *et al.* 2004**	United Kingdom	Areas with large field sizes	Apiformes	Bees	Cropland	Grass-sown or naturally regenerated field margin/set-	0.632	0.286

							aside		
40	Meek *et al*. 2002	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	-0.037	0.500
40	Meek *et al*. 2002	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	0.971	0.500
40	Meek *et al*. 2002	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Overall measure-type effect size	0.467	0.500
41	Merckx *et al*. 2009	United Kingdom	-	Lepidoptera	Larger moths	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.369	0.500
41	Merckx *et al*. 2009	United Kingdom	-	Lepidoptera	Larger moths	Cropland	Other	1.553	0.500
41	Merckx *et al*. 2009	United Kingdom	-	Lepidoptera	Larger moths	Cropland	Overall measure-type effect size	1.461	0.500
42	Muchow *et al.* 2007	Germany	-	Apiformes	Bees	Cropland	Sown flower strips	1.995	0.278
42	Muchow *et al.* 2007	Germany	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	2.054	0.278
43	Potts *et al*. 2009	United Kingdom	-	Apiformes	Bumblebees	Grassland	Grass-sown or naturally regenerated field margin/set-aside	0.357	0.167
43	Potts *et al*. 2009	United Kingdom	-	Apiformes	Bumblebees	Grassland	Sown flower strips	3.141	0.167
43	Potts *et al*. 2009	United Kingdom	-	Apiformes	Bumblebees	Grassland	Overall measure-type effect size	1.749	0.167
43	Potts *et al*. 2009	United Kingdom	-	Lepidoptera	Butterflies	Grassland	Grass-sown or naturally regenerated field margin/set-aside	0.716	0.167
43	Potts *et al*. 2009	United Kingdom	-	Lepidoptera	Butterflies	Grassland	Sown flower strips	1.893	0.167
43	Potts *et al*. 2009	United Kingdom	-	Lepidoptera	Butterflies	Grassland	Overall measure-type effect size	1.305	0.167
44	Power and Stout 2011	Ireland	-	Apiformes	Bees	Grassland	Organic farming	0.609	0.200

44	Power and Stout 2011	Ireland	-	Syrphidae	Hoverflies	Grassland	Organic farming	0.127	0.200
45	Pywell *et al.* 2005	United Kingdom	-	Apiformes	Bumblebees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	2.725	0.125
45	Pywell *et al.* 2005	United Kingdom	-	Apiformes	Bumblebees	Cropland	Sown flower strips	2.334	0.071
46	Pywell *et al.* 2006	United Kingdom	-	Apiformes	Bumblebees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.363	0.063
46	Pywell *et al.* 2006	United Kingdom	-	Apiformes	Bumblebees	Cropland	Sown flower strips	2.888	0.075
46	Pywell *et al.* 2006	United Kingdom	-	Apiformes	Bumblebees	Cropland	Overall measure-type effect size	2.058	0.069
47	Risberg 2004	Sweden	-	Apiformes	Bumblebees	Cropland	Organic farming	0.140	0.400
48	Roth *et al.* 2008	Switzerland	-	Lepidoptera	Butterflies	Cropland and grassland	Other	0.448	0.048
49	Rundlöf and Smith 2006	Sweden	Heterogeneous	Lepidoptera	Butterflies and Burnet moths	Cropland	Organic farming	0.561	0.333
49	Rundlöf and Smith 2006	Sweden	Homogeneous	Lepidoptera	Butterflies and Burnet moths	Cropland	Organic farming	1.890	0.333
50	Rundlöf *et al.* 2008a	Sweden	Heterogeneous	Apiformes	Bumblebees	Cropland	Organic farming	0.648	0.333
50	Rundlöf *et al.* 2008a	Sweden	Homogeneous	Apiformes	Bumblebees	Cropland	Organic farming	2.289	0.333
51	Rundlöf *et al.* 2008b	Sweden	-	Lepidoptera	Butterflies and Burnet moths	Cropland	Organic farming	3.867	0.250
52	Saarinen 2002	Finland	-	Lepidoptera	Butterflies	Grassland	Extensive grassland	-0.210	0.236
53	Sjödin *et al.* 2008	Sweden	-	Apiformes	Bees	Grassland	Extensive grassland	0.081	0.250
53	Sjödin *et al.* 2008	Sweden	-	Lepidoptera	Butterflies and Burnet moths	Grassland	Extensive grassland	-0.111	0.250
53	Sjödin *et al.* 2008	Sweden	-	Syrphidae	Hoverflies	Grassland	Extensive grassland	0.652	0.250

54	Steffan-Dewenter and Tscharntke 1997	Germany	-	Lepidoptera	Butterflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	5.942	0.500
54	Steffan-Dewenter and Tscharntke 1997	Germany	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	2.341	0.500
54	Steffan-Dewenter and Tscharntke 1997	Germany	-	Lepidoptera	Butterflies	Cropland	Overall measure-type effect size	4.141	0.500
55	Steffan-Dewenter and Tscharntke 2001	Germany	-	Apiformes	Bees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.425	0.500
55	Steffan-Dewenter and Tscharntke 2001	Germany	-	Apiformes	Bees	Cropland	Sown flower strips	-0.464	0.500
55	Steffan-Dewenter and Tscharntke 2001	Germany	-	Apiformes	Bees	Cropland	Overall measure-type effect size	0.481	0.500
56	Weibull *et al.* 2003	Sweden	-	Lepidoptera	Butterflies	Cropland	Organic farming	0.623	0.259
56	Weibull *et al.* 2003	Sweden	-	Lepidoptera	Butterflies	Grassland	Organic farming	0.000	0.250
56	Weibull *et al.* 2003	Sweden	-	Lepidoptera	Butterflies	Overall farmland type effect size	Organic farming	0.411	0.256
57	Weiner *et al.* 2011	Germany	-	Apiformes	Bees	Grassland	Extensive grassland	0.553	0.100
57	Weiner *et al.* 2011	Germany	-	Lepidoptera	Butterflies	Grassland	Extensive grassland	1.021	0.100
57	Weiner *et al.* 2011	Germany	-	Syrphidae	Hoverflies	Grassland	Extensive grassland	-0.219	0.100

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Table S2 Summary of data used in the pollinator abundance analyses. References for grey literature are shown underlined; references for the EASY data are shown in bold.

Study no.	**Source**	**Country**	**Region / landscape**	**Order / family**	**Species / group**	**Farmland type**	**Measure-type**	**Hedges' *d***	**NP var (*d*)**
1	Alanen *et al.* 2011	Finland	-	Apiformes	Bumblebees	Cropland	Sown flower strips	0.195	0.500
1	Alanen *et al.* 2011	Finland	-	Lepidoptera	Butterflies and diurnal moths	Cropland	Sown flower strips	0.608	0.500
2	Albrecht *et al.* 2007a	Switzerland	-	Apiformes	Bees	Grassland	Extensive grassland	1.622	0.154
2	Albrecht *et al.* 2007a	Switzerland	-	Lepidoptera	Butterflies	Grassland	Extensive grassland	0.524	0.154
2	Albrecht *et al.* 2007a	Switzerland	-	Syrphidae	Hoverflies	Grassland	Extensive grassland	1.018	0.154
3	Albrecht *et al.* 2007b	Switzerland	-	Apiformes	Solitary bees	Grassland	Extensive grassland	0.711	0.154
4	Albrecht *et al.* 2010	Switzerland	-	Apiformes	Bees	Grassland	Extensive grassland	1.086	0.083
5	Aviron *et al.* 2010	Switzerland	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	1.939	0.088
6	**Batary *et al.* 2010**	Hungary	Alkali	Apiformes	Bees	Grassland	Extensive grassland	0.134	0.286
6	**Batary *et al.* 2010**	Hungary	Meadow	Apiformes	Bees	Grassland	Extensive grassland	-0.294	0.286
6	**Batary *et al.* 2010**	Hungary	Heves	Apiformes	Bees	Grassland	Extensive grassland	0.015	0.286
7	Belfrage *et al.* 2005	Sweden	-	Apiformes	Bumblebees	Cropland and grassland	Organic farming	0.668	0.333
7	Belfrage *et al.* 2005	Sweden	-	Lepidoptera	Butterflies	Cropland and grassland	Organic farming	1.998	0.333
8	Blake *et al.* 2011a	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	0.951	0.333
9	Blake *et al.* 2011b	United Kingdom	-	Apiformes	Bumblebees	Cropland	Sown flower strips	1.412	0.333
10	Brittain *et al.* 2010	Italy	-	Apiformes	Solitary bees	Cropland	Organic farming	-0.003	0.333

10	Brittain *et al.* 2010	Italy	-	Lepidoptera	Butterflies	Cropland	Organic farming	0.440	0.333
11	Buys *et al.* 1997	The Netherlands	-	Apiformes	Bumblebees and honeybees	Cropland	Sown flower strips	1.358	0.041
11	Buys *et al.* 1997	The Netherlands	-	Apiformes	Bumblebees and honeybees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.609	0.077
11	Buys *et al.* 1997	The Netherlands	-	Apiformes	Bumblebees and honeybees	Cropland	Overall measure-type effect size	1.445	0.059
11	Buys *et al.* 1997	The Netherlands	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	1.245	0.041
11	Buys *et al.* 1997	The Netherlands	-	Lepidoptera	Butterflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.139	0.077
11	Buys *et al.* 1997	The Netherlands	-	Lepidoptera	Butterflies	Cropland	Overall measure-type effect size	1.208	0.059
11	Buys *et al.* 1997	The Netherlands	-	Syrphidae	Hoverflies	Cropland	Sown flower strips	2.199	0.077
11	Buys *et al.* 1997	The Netherlands	-	Syrphidae	Hoverflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	3.067	0.142
11	Buys *et al.* 1997	The Netherlands	-	Syrphidae	Hoverflies	Cropland	Overall measure-type effect size	2.503	0.110
12	Carvell *et al.* 2007	United Kingdom	-	Apiformes	Bumblebees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.497	0.333
12	Carvell *et al.* 2007	United Kingdom	-	Apiformes	Bumblebees	Cropland	Sown flower strips	3.216	0.333
12	Carvell *et al.* 2007	United Kingdom	-	Apiformes	Bumblebees	Cropland	Overall measure-type effect size	1.857	0.333
13	**Concepción *et al.* 2008**	Spain	Retuerta del Bullaque	Apiformes	Bees	Cropland	Other	-0.500	0.286
13	**Concepción *et al.* 2008**	Spain	Huecas	Apiformes	Bees	Cropland	Other	0.769	0.286
14	De Snoo and De Leeuw 1996	The Netherlands	-	Apiformes	Bees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.512	0.200

14	De Snoo and De Leeuw 1996	The Netherlands	-	Lepidoptera	Moths	Cropland	Grass-sown or naturally regenerated field margin/set-aside	-0.598	0.250
14	De Snoo and De Leeuw 1996	The Netherlands	-	Syrphidae	Hoverflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.553	0.200
15	De Snoo *et al.* 1998	The Netherlands	-	Lepidoptera	Butterflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.155	0.238
16	Dover 1999	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Other	0.731	0.333
17	Dover *et al.* 2000	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Other	1.554	0.194
18	Ekroos *et al.* 2008	Finland	-	Apiformes	Bumblebees	Cropland	Organic farming	0.341	0.092
18	Ekroos *et al.* 2008	Finland	-	Lepidoptera	Diurnal macrolepidoptera	Cropland	Organic farming	-0.191	0.092
19	Feber *et al.* 1996	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	2.380	0.250
19	Feber *et al.* 1996	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.099	0.250
19	Feber *et al.* 1996	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Overall measure-type effect size	1.740	0.250
20	Feber *et al.* 2007	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Organic farming	0.601	0.200
21	Fuentes-Montemayor *et al.* 2011	United Kingdom	-	Lepidoptera	Macromoths	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.301	0.125
21	Fuentes-Montemayor *et al.* 2011	United Kingdom	-	Lepidoptera	Macromoths	Cropland and grassland	Other	0.058	0.154
21	Fuentes-Montemayor *et al.* 2011	United Kingdom	-	Lepidoptera	Macromoths	Cropland and grassland	Sown flower strips	0.157	0.125
21	Fuentes-Montemayor *et al.* 2011	United Kingdom	-	Lepidoptera	Macromoths	Cropland and grassland	Overall measure-type effect size	0.212	0.132
22	Gabriel *et al.* 2010	United Kingdom	Coldspot	Apiformes	Bees	Cropland	Organic farming	0.338	0.250

22	Gabriel *et al*. 2010	United Kingdom	Coldspot	Apiformes	Bees	Grassland	Organic farming	0.416	0.250
22	Gabriel *et al*. 2010	United Kingdom	Coldspot	Apiformes	Bees	Overall farmland type effect size	Organic farming	0.377	0.250
22	Gabriel *et al*. 2010	United Kingdom	Hotspot	Apiformes	Bees	Cropland	Organic farming	0.170	0.250
22	Gabriel *et al*. 2010	United Kingdom	Hotspot	Apiformes	Bees	Grassland	Organic farming	-0.678	0.250
22	Gabriel *et al*. 2010	United Kingdom	Hotspot	Apiformes	Bees	Overall farmland type effect size	Organic farming	-0.254	0.250
22	Gabriel *et al*. 2010	United Kingdom	Coldspot	Syrphidae	Hoverflies	Cropland	Organic farming	-1.119	0.250
22	Gabriel *et al*. 2010	United Kingdom	Coldspot	Syrphidae	Hoverflies	Grassland	Organic farming	-1.101	0.250
22	Gabriel *et al*. 2010	United Kingdom	Coldspot	Syrphidae	Hoverflies	Overall farmland type effect size	Organic farming	-1.110	0.250
22	Gabriel *et al*. 2010	United Kingdom	Hotspot	Syrphidae	Hoverflies	Cropland	Organic farming	-0.630	0.250
22	Gabriel *et al*. 2010	United Kingdom	Hotspot	Syrphidae	Hoverflies	Grassland	Organic farming	-0.647	0.250
22	Gabriel *et al*. 2010	United Kingdom	Hotspot	Syrphidae	Hoverflies	Overall farmland type effect size	Organic farming	-0.638	0.250
23	Gathmann *et al*. 1994	Germany	-	Apiformes	Solitary bees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.555	0.500
23	Gathmann *et al*. 1994	Germany	-	Apiformes	Solitary bees	Cropland	Sown flower strips	0.847	0.500
23	Gathmann *et al*. 1994	Germany	-	Apiformes	Solitary bees	Cropland	Overall measure-type effect size	0.701	0.500
24	Goulson *et al*. 2002	United Kingdom	-	Apiformes	Bombus terrestris	Cropland	Grass-sown or naturally regenerated field margin/set-aside	-0.084	0.222
25	Haenke *et al*. 2009	Germany	-	Syrphidae	Hoverflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.873	0.286
25	Haenke *et al*. 2009	Germany	-	Syrphidae	Hoverflies	Cropland	Sown flower strips	2.576	0.286

25	Haenke *et al*. 2009	Germany	-	Syrphidae	Hoverflies	Cropland	Overall measure-type effect size	1.725	0.286
26	Harwood *et al*. 1994	United Kingdom	-	Syrphidae	Hoverflies	Cropland	Sown flower strips	2.450	0.333
27	Heard *et al*. 2007	United Kingdom	-	Apiformes	Bumblebees	Cropland	Sown flower strips	1.260	0.167
28	Hodgson *et al*. 2010	United Kingdom	Coldspot	Lepidoptera	Butterflies	Cropland	Organic farming	-0.025	0.250
28	Hodgson *et al*. 2010	United Kingdom	Coldspot	Lepidoptera	Butterflies	Grassland	Organic farming	-0.131	0.250
28	Hodgson *et al*. 2010	United Kingdom	Coldspot	Lepidoptera	Butterflies	Overall farmland type effect size	Organic farming	-0.078	0.250
28	Hodgson *et al*. 2010	United Kingdom	Hotspot	Lepidoptera	Butterflies	Cropland	Organic farming	0.130	0.250
28	Hodgson *et al*. 2010	United Kingdom	Hotspot	Lepidoptera	Butterflies	Grassland	Organic farming	0.648	0.268
28	Hodgson *et al*. 2010	United Kingdom	Hotspot	Lepidoptera	Butterflies	Overall farmland type effect size	Organic farming	0.380	0.259
29	**Holzschuh *et al.* 2007**	Germany	Göttingen-simple	Apiformes	Bees	Cropland	Organic farming	0.984	0.333
29	**Holzschuh *et al.* 2007**	Germany	Göttingen-complex	Apiformes	Bees	Cropland	Organic farming	1.097	0.333
29	**Holzschuh *et al.* 2007**	Germany	Soest	Apiformes	Bees	Cropland	Organic farming	1.333	0.333
29	**Holzschuh *et al.* 2007**	Germany	Marburg	Apiformes	Bees	Cropland	Organic farming	1.738	0.400
30	Holzschuh *et al.* 2010	Germany	-	Apiformes	Solitary bees	Cropland	Organic farming	0.372	0.087
31	Hopkins and Feber 1997	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	1.518	0.400
32	Jonason *et al*. 2011	Sweden	-	Lepidoptera	Butterflies	Cropland	Organic farming	0.861	0.075
33	Kells *et al*. 2001	United Kingdom	-	Apiformes	Bumblebees and Honeybees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	4.790	0.300

34	Kleijn *et al.* 1999	The Netherlands	-	Apiformes	Bees	Grassland	Extensive grassland	0.179	0.286
34	Kleijn *et al.* 1999	The Netherlands	-	Lepidoptera	Butterflies	Grassland	Extensive grassland	0.198	0.286
34	Kleijn *et al.* 1999	The Netherlands	-	Syrphidae	Hoverflies	Grassland	Extensive grassland	0.290	0.286
35	Kleijn *et al.* 2004	The Netherlands	Clay	Apiformes	Bees	Grassland	Extensive grassland	0.840	0.182
35	Kleijn *et al.* 2004	The Netherlands	Peat	Apiformes	Bees	Grassland	Extensive grassland	0.507	0.125
35	Kleijn *et al.* 2004	The Netherlands	Sand	Apiformes	Bees	Grassland	Extensive grassland	-0.086	0.200
35	Kleijn *et al.* 2004	The Netherlands	Clay	Syrphidae	Hoverflies	Grassland	Extensive grassland	0.115	0.182
35	Kleijn *et al.* 2004	The Netherlands	Peat	Syrphidae	Hoverflies	Grassland	Extensive grassland	0.784	0.125
35	Kleijn *et al.* 2004	The Netherlands	Sand	Syrphidae	Hoverflies	Grassland	Extensive grassland	0.723	0.200
36	**Kleijn *et al.* 2006**	The Netherlands	Eempolder	Apiformes	Bees	Grassland	Extensive grassland	-0.732	0.286
36	**Kleijn *et al.* 2006**	The Netherlands	Utrechtse en Hollandse Venen	Apiformes	Bees	Grassland	Extensive grassland	0.667	0.286
36	**Kleijn *et al.* 2006**	The Netherlands	Alblasserwaard and Vijfheerenlanden	Apiformes	Bees	Grassland	Extensive grassland	-0.208	0.286
37	Knop *et al.* 2006	Switzerland	Ruswill	Apiformes	Bees	Grassland	Extensive grassland	-0.895	0.286
37	Knop *et al.* 2006	Switzerland	Bauma	Apiformes	Bees	Grassland	Extensive grassland	-0.574	0.286
37	Knop *et al.* 2006	Switzerland	Flühli	Apiformes	Bees	Grassland	Extensive grassland	0.367	0.286
38	Kohler *et al.* 2008	The Netherlands	-	Apiformes	Bees	Grassland	Sown flower strips	2.039	0.220
38	Kohler *et al.* 2008	The Netherlands	-	Syrphidae	Hoverflies	Grassland	Sown flower strips	2.817	0.220

39	Kovács-Hostyánszki *et al.* 2011a	Hungary	-	Apiformes	Bees	Cropland	Other	1.199	0.250
40	Kovács-Hostyánszki *et al.* 2011b	Hungary	-	Apiformes	Bees	Cropland	Sown flower strips	-0.166	0.229
40	Kovács-Hostyánszki *et al.* 2011b	Hungary	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	3.239	0.229
41	Krauss *et al.* 2011	Germany	-	Apiformes	Bumblebees	Cropland	Organic farming	1.341	0.133
41	Krauss *et al.* 2011	Germany	-	Lepidoptera	Butterflies	Cropland	Organic farming	0.987	0.133
41	Krauss *et al.* 2011	Germany	-	Syrphidae	Hoverflies	Cropland	Organic farming	1.022	0.133
42	Kruess and Tscharntke 2002	Germany	-	Apiformes	Bees	Grassland	Extensive grassland	0.426	0.367
42	Kruess and Tscharntke 2002	Germany	-	Lepidoptera	Butterflies and Burnet moths	Grassland	Extensive grassland	1.927	0.333
43	Kuussaari *et al.* 2011	Finland	-	Apiformes	Bumblebees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	2.174	0.500
43	Kuussaari *et al.* 2011	Finland	-	Lepidoptera	Butterflies and diurnal moths	Cropland	Grass-sown or naturally regenerated field margin/set-aside	3.479	0.500
44	Kvarnbäck 2009	Sweden	-	Apiformes	Bumblebees	Cropland	Sown flower strips	0.625	0.400
44	Kvarnbäck 2009	Sweden	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	1.164	0.400
45	Lagerlöf and Wallin 1993	Sweden	-	Apiformes	Bees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.755	0.500
45	Lagerlöf and Wallin 1993	Sweden	-	Apiformes	Bees	Cropland	Sown flower strips	-0.214	0.500
45	Lagerlöf and Wallin 1993	Sweden	-	Apiformes	Bees	Cropland	Overall measure-type effect size	0.270	0.500
45	Lagerlöf and Wallin 1993	Sweden	-	Lepidoptera	Butterflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.530	0.500

45	Lagerlöf and Wallin 1993	Sweden	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	1.433	0.500
45	Lagerlöf and Wallin 1993	Sweden	-	Lepidoptera	Butterflies	Cropland	Overall measure-type effect size	1.481	0.500
45	Lagerlöf and Wallin 1993	Sweden	-	Syrphidae	Hoverflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	-0.936	0.500
45	Lagerlöf and Wallin 1993	Sweden	-	Syrphidae	Hoverflies	Cropland	Sown flower strips	-1.186	0.500
45	Lagerlöf and Wallin 1993	Sweden	-	Syrphidae	Hoverflies	Cropland	Overall measure-type effect size	-1.061	0.500
46	Littlewood *et al.* 2008	United Kingdom	-	Lepidoptera	Nocturnal moths	Grassland	Extensive grassland	0.723	0.333
47	Lye *et al.* 2009	United Kingdom	-	Apiformes	Bumblebees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.543	0.400
47	Lye *et al.* 2009	United Kingdom	-	Apiformes	Bumblebees	Cropland and grassland	Other	0.275	0.400
47	Lye *et al.* 2009	United Kingdom	-	Apiformes	Bumblebees	Cropland and grassland	Overall measure-type effect size	0.409	0.400
48	MacLeod 1999	United Kingdom	-	Syrphidae	Episyrphus balteatus	Cropland	Sown flower strips	0.951	0.250
49	Mand *et al.* 2001	Estonia	-	Apiformes	Bumblebees	Cropland and grassland	Organic farming	0.789	0.167
50	**Marshall *et al.* 2004**	United Kingdom	Areas with small field sizes	Apiformes	Bees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.228	0.286
50	**Marshall *et al.* 2004**	United Kingdom	Areas with intermediate field sizes	Apiformes	Bees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.214	0.286
50	**Marshall *et al.* 2004**	United Kingdom	Areas with large field sizes	Apiformes	Bees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.466	0.286
51	Meek *et al.* 2002	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.703	0.500
51	Meek *et al.* 2002	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	3.096	0.500

51	Meek *et al.* 2002	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Overall measure-type effect size	1.899	0.500
52	Merckx *et al.* 2009	United Kingdom	-	Lepidoptera	Larger moths	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.225	0.500
52	Merckx *et al.* 2009	United Kingdom	-	Lepidoptera	Larger moths	Cropland	Other	0.562	0.500
52	Merckx *et al.* 2009	United Kingdom	-	Lepidoptera	Larger moths	Cropland	Overall measure-type effect size	0.394	0.500
53	Muchow *et al.* 2007	Germany	-	Apiformes	Bees	Cropland	Sown flower strips	1.970	0.278
53	Muchow *et al.* 2007	Germany	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	1.488	0.278
54	Potts *et al.* 2009	United Kingdom	-	Apiformes	Bumblebees	Grassland	Grass-sown or naturally regenerated field margin/set-aside	0.407	0.167
54	Potts *et al.* 2009	United Kingdom	-	Apiformes	Bumblebees	Grassland	Sown flower strips	1.705	0.167
54	Potts *et al.* 2009	United Kingdom	-	Apiformes	Bumblebees	Grassland	Overall measure-type effect size	1.056	0.167
54	Potts *et al.* 2009	United Kingdom	-	Lepidoptera	Butterflies	Grassland	Grass-sown or naturally regenerated field margin/set-aside	0.566	0.167
54	Potts *et al.* 2009	United Kingdom	-	Lepidoptera	Butterflies	Grassland	Sown flower strips	1.712	0.167
54	Potts *et al.* 2009	United Kingdom	-	Lepidoptera	Butterflies	Grassland	Overall measure-type effect size	1.139	0.167
55	Power and Stout 2011	Ireland	-	Apiformes	Bees	Grassland	Organic farming	1.160	0.200
55	Power and Stout 2011	Ireland	-	Syrphidae	Hoverflies	Grassland	Organic farming	2.069	0.200
56	Pywell *et al.* 2005	United Kingdom	-	Apiformes	Bumblebees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.199	0.125
56	Pywell *et al.* 2005	United Kingdom	-	Apiformes	Bumblebees	Cropland	Sown flower strips	1.149	0.071

57	Pywell *et al.* 2006	United Kingdom	-	Apiformes	Bumblebees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.818	0.063
57	Pywell *et al.* 2006	United Kingdom	-	Apiformes	Bumblebees	Cropland	Sown flower strips	1.216	0.075
57	Pywell *et al.* 2006	United Kingdom	-	Apiformes	Bumblebees	Cropland	Overall measure-type effect size	0.999	0.069
58	Pywell *et al.* 2007	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	1.448	0.333
58	Pywell *et al.* 2007	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	1.605	0.333
58	Pywell *et al.* 2007	United Kingdom	-	Lepidoptera	Butterflies	Cropland	Overall measure-type effect size	1.526	0.333
59	Risberg 2004	Sweden	-	Apiformes	Bumblebees	Cropland	Organic farming	1.996	0.400
60	Rundlöf and Smith 2006	Sweden	Heterogeneous	Lepidoptera	Butterflies and Burnet moths	Cropland	Organic farming	0.559	0.333
60	Rundlöf and Smith 2006	Sweden	Homogeneous	Lepidoptera	Butterflies and Burnet moths	Cropland	Organic farming	2.093	0.333
61	Rundlöf *et al.* 2008a	Sweden	Heterogeneous	Apiformes	Bumblebees	Cropland	Organic farming	0.297	0.333
61	Rundlöf *et al.* 2008a	Sweden	Homogeneous	Apiformes	Bumblebees	Cropland	Organic farming	2.478	0.333
62	Rundlöf *et al.* 2008b	Sweden	-	Lepidoptera	Butterflies and Burnet moths	Cropland	Organic farming	3.346	0.250
63	Saarinen 2002	Finland	-	Lepidoptera	Butterflies	Grassland	Extensive grassland	0.039	0.236
64	Sjödin *et al.* 2008	Sweden	-	Apiformes	Bees	Grassland	Extensive grassland	0.484	0.250
64	Sjödin *et al.* 2008	Sweden	-	Lepidoptera	Butterflies and Burnet moths	Grassland	Extensive grassland	0.011	0.250
64	Sjödin *et al.* 2008	Sweden	-	Syrphidae	Hoverflies	Grassland	Extensive grassland	0.436	0.250
65	Steffan-Dewenter and Tscharntke 1997	Germany	-	Lepidoptera	Butterflies	Cropland	Grass-sown or naturally regenerated field margin/set-aside	3.365	0.500

65	Steffan-Dewenter and Tscharntke 1997	Germany	-	Lepidoptera	Butterflies	Cropland	Sown flower strips	1.603	0.500
65	Steffan-Dewenter and Tscharntke 1997	Germany	-	Lepidoptera	Butterflies	Cropland	Overall measure-type effect size	2.484	0.500
66	Steffan-Dewenter and Tscharntke 2001	Germany	-	Apiformes	Bees	Cropland	Grass-sown or naturally regenerated field margin/set-aside	0.545	0.500
66	Steffan-Dewenter and Tscharntke 2001	Germany	-	Apiformes	Bees	Cropland	Sown flower strips	1.148	0.500
66	Steffan-Dewenter and Tscharntke 2001	Germany	-	Apiformes	Bees	Cropland	Overall measure-type effect size	0.846	0.500
67	Weibull *et al.* 2003	Sweden	-	Lepidoptera	Butterflies	Cropland	Organic farming	0.341	0.259
67	Weibull *et al.* 2003	Sweden	-	Lepidoptera	Butterflies	Grassland	Organic farming	0.303	0.250
67	Weibull *et al.* 2003	Sweden	-	Lepidoptera	Butterflies	Overall farmland type effect size	Organic farming	0.328	0.256
68	Weiner *et al.* 2011	Germany	-	Apiformes	Bees	Grassland	Extensive grassland	0.683	0.100
68	Weiner *et al.* 2011	Germany	-	Lepidoptera	Butterflies	Grassland	Extensive grassland	0.889	0.100
68	Weiner *et al.* 2011	Germany	-	Syrphidae	Hoverflies	Grassland	Extensive grassland	-0.165	0.100
69	Wickramasinghe *et al.* 2004	United Kingdom	-	Lepidoptera	Nocturnal moths	Cropland and grassland	Organic farming	0.482	0.083

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Table S3. Regression coefficients and heterogeneity statistics for the continuous meta-analyses of the relationship between (contrasts) in resource availability and effects of agri-environmental measures on bee abundance in croplands and grasslands. *P*-values < 0.05 are shown in bold. Variation explained by the model (r^2) is shown for significant regressions.

Continuous variable	**Slope**	**SE**	Q_M	***P***	r^2
Cropland					
Contrast in forb species richness	0.066	0.028	5.691	**0.017**	0.53
Forb species richness in control fields	-0.032	0.014	5.118	**0.024**	0.48
Contrast in forb cover	0.075	0.039	3.616	0.057	
Forb cover in control fields	-0.019	0.012	2.660	0.103	
Grassland					
Contrast in forb species richness	-0.034	0.030	1.234	0.267	
Forb species richness in control fields	0.007	0.021	0.110	0.741	
Contrast in forb cover	0.029	0.024	1.474	0.225	
Forb cover in control fields	-0.015	0.013	1.304	0.254	

CHAPTER 5

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

Photo: Jennifer Wickens

Jeroen Scheper[1], Riccardo Bommarco[2], Andrea Holzschuh[3],
Simon G. Potts[4], Verena Riedinger[3], Stuart P.M. Roberts[4], Maj Rundlöf[5],
Henrik G. Smith[5], Ingolf Steffan-Dewenter[3], Jennifer B. Wickens[4],
Victoria J. Wickens[4] & David Kleijn[1,6]

[1]Alterra, Animal Ecology Team, 6700 AA Wageningen, The Netherlands; [2]Swedish University of Agricultural Sciences, Department of Ecology, 750 07 Uppsala, Sweden; [3]Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am Hubland, 97074 Würzburg, Germany; [4]School of Agriculture, Policy and Development, University of Reading, Reading, RG6 6AR, UK; [5]Lund University, Department of Biology & Centre of Environmental and Climate Research, 223 62 Lund, Sweden; [6]Wageningen University, Resource Ecology Group, 6700 AA Wageningen, The Netherlands

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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. While such measures generally enhance bee diversity, effectiveness varies considerably between landscapes and regions. We hypothesise 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 (BACI) approach to analyse 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 decreased with increasing amount of alternative floral resources in the landscape, whereas effects on bumblebees increased with increasing early-season landscape-wide floral resource availability, reflecting their dependence on seasonal continuity of food resources.
4. The increased bee densities in wildflower strips generally levelled off in the second year after establishment of the strips, suggesting that the positive effects of wildflower strips mainly reflected spatio-temporal behavioural foraging responses rather than population effects.
5. *Synthesis and applications.*
   Our study shows that the effects of wildflower strips on bees are largely driven by the extent to which flower richness is increased. The effectiveness of this measure could therefore be enhanced by maximizing the number of bee forage species in seed mixtures used for wildflower strip establishment. Furthermore, sustained positive effects on bees require management regimes that effectively maintain flower richness in the strips through the years. Further research is required to determine whether, and under what conditions, such created habitats result in actual population-level effects.

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 extensifying 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 is 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), i.e. 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 be mainly mediated through effects on 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, most studies examining effects of mitigation measures provide one-year “snap shot” comparisons of species richness and abundance of foraging pollinators in sites with and without measures. This makes it impossible to disentangle small-scale spatio-temporal foraging responses, resulting from concentration processes, from actual population level responses (Kleijn *et al.* 2011). The establishment of flower-rich habitats in agricultural landscapes may cause the local pool of bees to aggregate on these resource-rich patches (Veddeler, Klein & Tscharntke 2006). Whether responses in such studies are (partly) caused by increases in bee populations remains to be determined. In order to detect actual population increases, monitoring of measures should be performed over several years, in mitigation and control sites located in spatially independent landscapes, while taking into account any initial between-site differences (Kleijn & Sutherland 2003). 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 three-year Before–After Control-Impact (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 i) whether 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, iii) whether the importance of environmental factors differs between bumblebees and solitary bees, and iv) to what extent observed bee responses indicate population-level effects. 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 spring 2011, we selected 16 field boundaries adjacent to conventionally managed arable fields in each country. Field boundaries 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.

In the autumn of 2011 we established wildflower strips alongside focal field boundaries in half of the 16 study landscapes in each country; the remaining half served as control sites. Strips (100 m x 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. 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%). Flower strips were not fertilized or managed during the two years after their establishment.

Study landscapes, defined as the area in a 1 km radius around each field boundary and wildflower strip, covered a gradient of land use intensity (annual nitrogen input per hectare agricultural land in the landscape), landscape complexity (percentage semi-natural habitat and landscape-wide floral resource availability (see section “Quantifying landscape characteristics” below). With the exception of 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) in the UK, means for landscape context variables were similar for treatment and control landscapes (Table S1). Across countries, landscape variables were only weakly correlated (all $|r| < 0.32$).

SURVEYING BEES AND FLOWERING PLANTS

In 2011, the year before the wildflower strips were established, control field boundaries and field boundaries bordering the future wildflower strips (hereafter referred to as pre-treatment field boundaries) were surveyed for baseline data on bees 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 failed to establish due to very wet weather and this site was therefore excluded from the analysis.

We sampled bees using standardised transect walks in two contiguous 150 m^2 transects (15 minutes pure collecting time per transect), and recorded flower cover and species richness of flowering forb species in each transect. Dimensions of transects in wildflower strips were 50 m × 3 m; dimensions of transects in control field boundaries varied according to the size of the field boundaries, with widths ranging between 1 m and 3 m. Surveys were carried out between 9:00 and 18:00 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 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 was 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) 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 site 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 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 solitary bees separately. Although some halictid bee species display primitively 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 × year as fixed factors and study site as random factor. Model significance was assessed using backward model simplification and likelihood ratio tests. For models with significant treatment × year interactions, we used non-orthogonal contrasts to decompose the interaction into separate treatment × 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 and would 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 offset.

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 $\frac{X_{2013}}{X_{2011}}$, 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 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 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 1) the environmental factor only, 2) the additive effect of the environmental factor and treatment, or 3) 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 hypothesized 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.

There were systematic differences between UK treatment and control study sites in terms of percentage 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 % semi-natural habitat and early floral resource availability were not confounded with treatment. Results of the analysis on the full dataset 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 wildflower 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 in Supporting Information; Table 1; Table S3). Establishment of 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 in Supporting Information; Table S3).

EFFECTS OF WILDFLOWER STRIPS ON BEE ABUNDANCE AND SPECIES RICHNESS

In total 5,768 bumblebees and 1,405 solitary bees were observed across three 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*, (1,686 individuals) *B. terrestris/lucorum* complex (1,429) and *B. pascuorum* (1,112) were the most abundant bumblebee species, and *Lasioglossum villosulum* (124), *L. 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 × 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. 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; Table 1; Table S3).

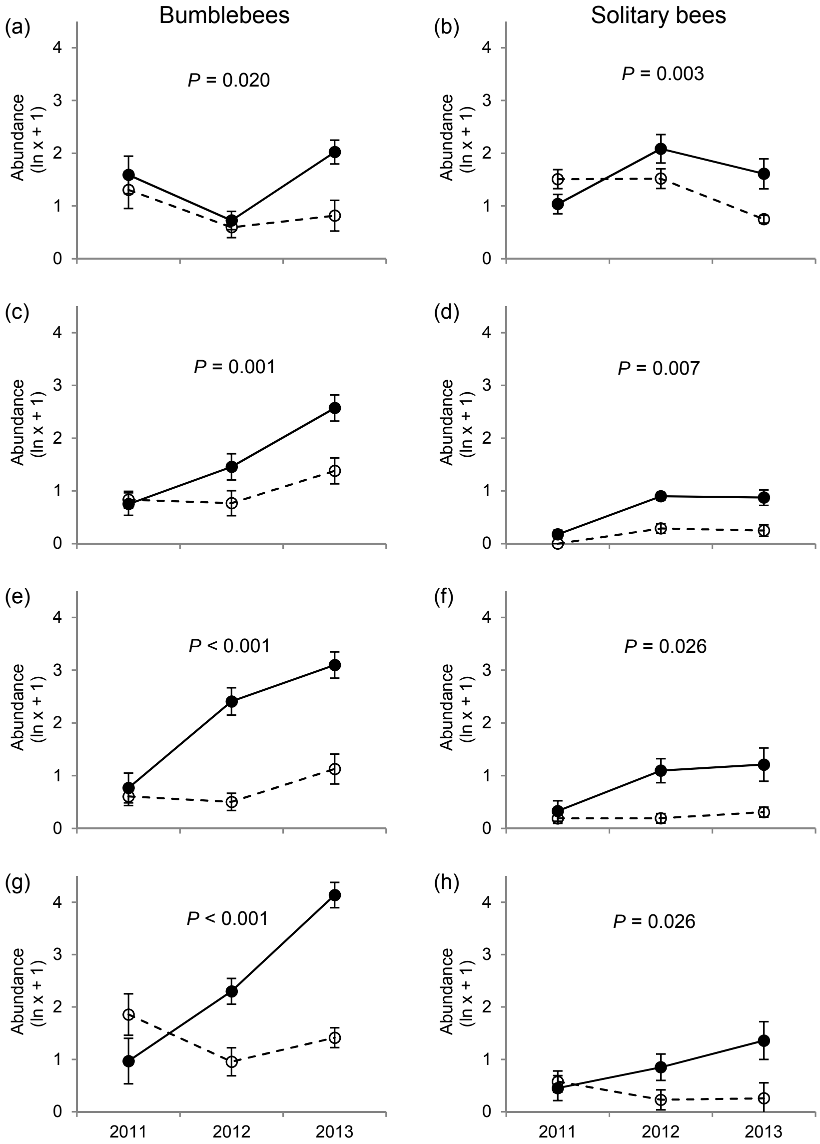

Figure 1. Mean abundance of bumblebees and solitary bees in wildflower strips (filled circles, solid lines) and control field boundaries (open circles, dashed lines) in Germany (a, b), Sweden (c, d), The Netherlands (e, f) and the UK (g, h). Error bars represent SE. *P*-values indicate significance of treatment × year interactions (see Table 1).

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 × year interactions are shown in bold

	Germany		**Sweden**		**Netherlands**		**UK**	
	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
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**

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 × year × 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 × 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 (Fig. 1; Fig. S2).

Overall, very few individuals of Red Listed bee species were observed over the three 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 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

Table 2. Candidate models (Δ AIC$_c$ < 2) explaining the relative change in bee abundance and richness in wildflower strips and control sites between 2011 and 2013. Models are ranked in order of increasing differences in corrected Akaike information criterion (Δ AICc). Regression coefficients, standardized by centering and dividing by 2 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

	Explanatory variable										**DF**	**AIC$_c$**	**Δ AIC$_c$**	**ω**
Response variable	T	FR	RES_{Early}	RES_{Late}	N	SNH	T × FR	FR × RES_{Early}	T × RES_{Early}	T × RES_{Late}				
Bumblebees														
abundance	1.28	0.94	0.36						1.41		7	159.6	0.00	1.00
richness	0.37	0.69	0.22						0.59		7	78.9	0.00	0.68
	0.36	0.19	0.19					0.31	0.49		8	80.4	1.50	0.32
Solitary bees														
abundance	0.66	0.66		-0.06						-0.93	7	118.0	0.00	1.00
richness	0.31	0.25									5	59.1	0.00	0.27
	0.41										4	59.1	0.00	0.27
	0.28	0.31		0.16							6	60.5	1.46	0.13
	0.31	0.25					-0.20				6	60.7	1.60	0.12
	0.40				0.11						5	60.8	1.77	0.11
	0.41					0.07					5	61.0	1.99	0.10

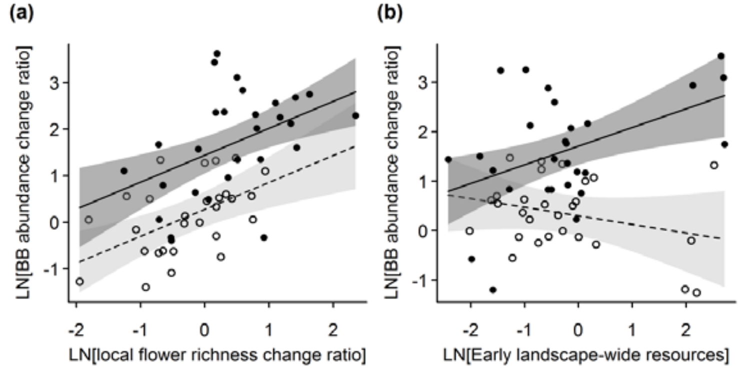

Figure 2. Conditional partial regression plots for the best model explaining the relative change in bumblebee (BB) abundance between 2011 and 2013 (see Table 3): (a) effects of local relative change in flower richness between 2011 and 2013, and (b) interacting effects of treatment (wildflower strips, 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 bumblebee abundance. Plotted points are partial residuals; shaded areas indicate 95% confidence intervals.

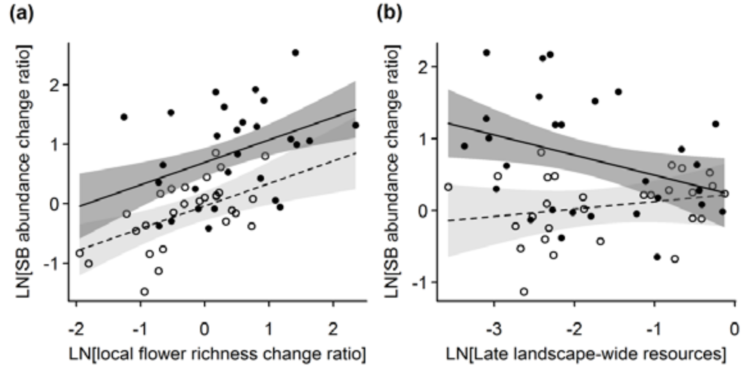

Figure 3. Conditional partial regression plots for the best model explaining the relative change in solitary bee (SB) abundance between 2011 and 2013 (see Table 3): (a) effects of local relative change in flower richness between 2011 and 2013, and (b) interacting effects of treatment (wildflower strips, 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 solitary bee abundance. Plotted points are partial residuals; shaded areas indicate 95% confidence intervals.

interaction effects of treatment and early landscape-wide floral resource availability also best explained changes in bumblebee richness in sites (ω = 0.67, 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 (ω = 1.00, Table 2). This model resembled the models for bumblebees with respect to the positive effects of local change in flower richness (Fig. 3a). However, in contrast to the positive interaction effect of treatment and early-season landscape-wide floral resource availability on changes in bumblebees, the effect of treatment on changes in solitary bee abundance depended on late-season floral resources availability, and was negative: differences between wildflower strips and control sites decreased with increasing late-season landscape-wide floral resource availability (Fig. 3b). There was considerable uncertainty associated with the selection of the model best explaining the results for changes in solitary bee richness (Table 2). The highest ranked model, which included the factors treatment and local change in flower richness, hardly performed better than the second-best treatment-only model (Δ AIC$_c$ = 0.003).

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. By and large, variation in local and landscape-wide floral resources explained differences between the effect sizes of wildflowers 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 (Fig. 2; Fig. S3), whereas for solitary bees effects decreased with increasing late-season landscape-wide resource availability (Fig. 3).

Enhanced bee richness and abundance in wildflower strips (Fig. 1; Fig. 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. In line with Pywell *et al.* (2012), we found that measures designed to the needs of the targeted species group may promote both threatened and common species (Table S4) while effects of more widely implemented general agri-environmental extensification measures are generally restricted to common bee species (Kleijn *et al.* 2006).

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 decreased with increasing late-season landscape-wide floral resource availability (Fig. 3). This negative modulating effect of late landscape-wide floral resource availability probably reflects 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 & Tscharntke 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 (Fig. 2; Fig. 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 higher production of workers (Westphal, Steffan-Dewenter & Tscharntke 2009; Williams, Regetz & Kremen 2012). The larger effects of wildflower strips in landscapes with more early-flowering resources therefore probably result from temporal spill-over 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 landscape-wide floral resources during peak flowering of the strips (Carvell *et al.* 2011), we found no support for this in our study (Δ AIC_c of highest ranked model including interaction with late-season landscape-wide resources for bumblebee abundance = 8.50; richness = 7.95). This indicates that bumblebee responses to wildflower strips were more sensitive to early than to late-season landscape-wide floral resource availability.

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).

We failed to unequivocally demonstrate 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 population size or of a foraging response to the steadily increasing floral resources in the UK strips (Fig. 1g; Fig. S1g,h). In the other countries the effect sizes of bee responses were similar in the two years after wildflower strip establishment. This suggests that in 2012 the experimentally enhanced bee forage in the wildflower strips was insufficient to noticeably enhance their reproductive output and therefore bee numbers in 2013. We cannot altogether rule out population-level effects, as bee densities may have been enhanced 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 primarily reflect spatio-temporal behavioural responses. This may indicate that the increased floral resources in wildflower strips were still insufficient to boost bee populations, possibly due to the small size of the strips (300 m^2) or the limited duration of the study. 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 flower richness was increased by wildflower strip establishment was a strong predictor of their effectiveness, 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, preferably by including Fabaceae and Lamiaceae species that are the preferred host plants of many declining bee species (Scheper *et al.* 2014). 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. Besides establishing more botanically diverse and better maintained 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 semi-natural habitats would be adapted to facilitate 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.

Our study shows that for mobile invertebrate species population-level effects of conservation management are difficult to infer, even from multi-year, 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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SUPPORTING INFORMATION

Appendix S1. Methods for quantification of landscape-wide floral resource availability.
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 dataset, 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.
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Figure S2. Mean species richness of bumblebees and solitary bees in flower strips and control field boundaries.
Figure S3. Conditional partial regression plots for the best model explaining the relative change in bumblebee richness between 2011 and 2013.

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

We used a stratified sampling approach to estimate floral resource availability in the study landscapes. Flower inventories were conducted for up to seven main land use classes: semi-natural habitats, cultivated grasslands, non-mass flowering crop fields (e.g. maize fields, wheat fields), mass-flowering crop fields (e.g. oilseed rape fields), uncultivated field boundaries (e.g. ditch banks, road verges), non-flowering perennial habitats (e.g. forest interiors, vineyards) and gardens. Depending on the relative cover of the habitats in the different land use classes, flower inventories in plots of 100 m^2 were performed in three to eight randomly selected study landscapes per habitat type (total of 48 plots per country). Flower resource inventories were carried out twice a year, once before (in May) and once during (in July – August) peak flowering of the wildflower strips. We calculated the total landscape-wide floral resource availability (% cover) in May and July-August in each landscape as:

$$\frac{\sum_{i=1}^{n} PF_i \times PA_i}{100}$$

with PF_i representing the mean percentage flower cover in land use class i, PA_i the percentage area cover of land use class i in the landscape, and n the total number of land use classes in the landscape. Over the three year period, resource availability in May was strongly correlated with the percentage of mass-flowering oilseed rape in the landscapes (Germany $r = 0.86$; Sweden $r = 0.68$; Netherlands $r = 0.64$; UK $r = 0.89$).

Appendix S2. References for conservation status of bee species

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Table S1. Means (± standard errors) and ranges (in parentheses) for annual nitrogen input in agricultural fields, proportion of semi-natural habitat and estimated flower cover in landscapes surrounding (1 km radius) wildflower strips and control field boundaries in the four study countries in 2011 - 2013

	N input (kg^{-1} ha^{-1} $year^{-1}$)	**Semi-natural habitat (%)**	**Flower cover in May (%)**	**Flower cover in July – August (%)**
Germany				
Control	138.7 ± 13.9 (88.6 – 221.2)	11.6 ± 2.8 (1.9 – 25.9)	0.95 ± 0.11 (0.32 – 1.91)	0.06 ± 0.01 (0.03 – 0.11)
Flower strip	148.1 ± 9.4 (115.6 – 197.1)	9.8 ± 2.2 (1.5 – 18.2)	0.73 ± 0.14 (0.05 – 1.71)	0.05 ± 0.01 (0.02 – 0.07)
Sweden				
Control	113.5 ± 9.3 (78.8 – 146.9)	7.8 ± 2.0 (2.9 – 20.6)	0.55 ± 0.08 (0.18 – 0.99)	0.51 ± 0.05 (0.30 – 0.78)
Flower strip	116.0 ± 8.8 (67.3 – 140.9)	8.8 ± 1.6 (2.8 – 13.9)	0.66 ± 0.11 (0.19 – 1.16)	0.59 ± 0.07 (0.29 – 1.19)
Netherlands				
Control	215.5 ± 16.0 (158.5 – 279.0)	5.3 ± 0.7 (2.4 – 9.2)	0.23 ± 0.03 (0.04 – 0.44)	0.08 ± 0.01 (0.02 – 0.15)
Flower strip	227.7 ± 14.3 (162.0 – 276.8)	7.3 ± 1.3 (2.1 – 13.5)	0.39 ± 0.07 (0.08 – 0.83)	0.12 ± 0.02 (0.02 – 0.51)
UK				
Control	129.2 ± 16.2 (59.3 – 183.8)	20.9 ± 3.6 (1.8 – 45.0)	7.24 ± 0.96 (0.02 – 19.74)	0.16 ± 0.10 (0.02 – 2.55)
Flower strip	155.1 ± 11.1 (60.1 – 190.5)	5.4 ± 1.0 (1.7 – 9.0)	13.72 ± 1.54 (0.01 – 28.87)	0.11 ± 0.05 (0.01 – 9.06)

Table S2. Candidate models (Δ $AIC_c < 2$) explaining the relative change in bee abundance and richness in wildflower strips and control sites between 2011 and 2013, based on the full dataset, including the six deviating UK study sites. Models are ranked in order of increasing differences in corrected Akaike information criterion (Δ AICc). Regression coefficients, standardized by centering and dividing by 2 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, FC = relative change in local flower cover between 2011 vs 2013, RES_{Early} = landscape-wide floral resource availability in May, RES_{Late} = landscape-wide floral resource availability in July - August, SNH = proportion semi-natural habitat

	Predictor												**DF**	**AIC_c**	**Δ AIC_c**	**ω**
Response variable	T	FR	FC	RES_{May}	RES_{July}	SNH	SNH^2	T × FR	T × FC	T × RES_{May}	T × RES_{July}	T × SNH^2				
Bumblebees																
abundance	1.43	0.92		0.40						1.68			7	174.2	0.00	1.00
richness	0.44	0.66		0.14						0.66			7	85.8	0.00	1.00
Solitary bees																
abundance	0.84					0.35	-0.79						6	138.4	0.00	0.65
	0.73	0.55						-0.83					6	139.7	1.24	0.35
richness	0.51					0.00	-1.03					-1.53	8	67.3	0.00	0.14
	0.28	0.31			0.24			-0.39					7	67.8	0.51	0.11
	0.31		0.20										5	67.9	0.52	0.11
	0.38					0.15	-0.30						6	67.9	0.60	0.10
	0.42												4	67.9	0.62	0.10
	0.32	0.23											5	68.0	0.65	0.10
	0.32	0.25						-0.33					6	68.1	0.78	0.09
	0.29	0.27			0.21								6	68.5	1.12	0.08
	0.38		0.10						-0.38				6	68.5	1.13	0.08
	0.29	0.29			0.21						-0.25		7	69.3	1.92	0.05
	0.42				0.18								5	69.3	1.98	0.05

Table S3. Results of contrasts decomposing interaction effects of treatment and year on flower cover and richness, bumblebee abundance and richness, and solitary bee abundance and richness in each country. Contrasts for significant treatment × year interactions (Table 2) are given for the periods 2011 vs. 2012 and 2012 vs. 2013. Significant contrasts for treatment × year interactions are shown in bold

	Germany		Sweden		Netherlands		UK	
	t	*P*	*t*	*P*	*t*	*P*	*t*	*P*
Flower cover								
treatment × 2011-2012	-0.63	0.536	1.82	0.079	4.69	**<0.001**	1.57	0.130
treatment × 2012-2013	3.03	**0.005**	0.88	0.385	-0.44	0.662	3.16	**0.004**
Flower richness								
treatment × 2011-2012	-	-	-1.51	0.142	6.01	**<0.001**	1.42	0.167
treatment × 2012-2013	-	-	6.18	**<0.001**	-2.37	**0.025**	2.16	**0.041**
Bumblebee abundance								
treatment × 2011-2012	-0.38	0.708	2.33	**0.028**	3.88	**0.001**	4.30	**<0.001**
treatment × 2012-2013	2.58	**0.016**	1.51	0.141	0.15	0.884	2.66	**0.013**
Bumblebee richness								
treatment × 2011-2012	-	-	-	-	4.14	**<0.001**	3.35	**0.003**
treatment × 2012-2013	-	-	-	-	-0.34	0.733	2.57	**0.017**
Solitary bee abundance								
treatment × 2011-2012	2.50	**0.019**	2.72	**0.011**	2.32	**0.028**	1.64	0.114
treatment × 2012-2013	0.71	0.485	0.08	0.933	0.00	0.998	1.07	0.294
Solitary bee richness								
treatment × 2011-2012	2.37	**0.025**	1.32	0.198	2.30	**0.029**	2.44	**0.022**
treatment × 2012-2013	-0.36	0.720	0.51	0.612	-0.32	0.754	-0.26	0.794

Table S4. Results of generalized linear models comparing the abundance and species richness of Red Listed bee species in wildflower strips and control sites. Results are for combined 2012 and 2013 data per site. Mean abundance and species richness values (± SE) are shown. Significant *P*-values are shown in bold

	Germany	Sweden	Netherlands	UK
Abundance				
control	3.4 ± 0.6	0.4 ± 0.3	0.3 ± 0.3	0.00
flower strip	5.8 ± 0.8	0.8 ± 0.4	1.4 ± 0.5	2.4 ± 0.7
χ^2	6.30	1.02	7.45	25.91
P	**0.012**	0.431	**0.006**	**<0.001**
Species richness				
control	2.3 ± 0.5	0.3 ± 0.2	0.3 ± 0.3	0.00
flower strip	3.1 ± 0.4	0.4 ± 0.2	0.8 ± 0.3	1.4 ± 0.2
χ^2	1.64	0.20	2.36	15.24
P	0.200	0.654	0.125	**<0.001**

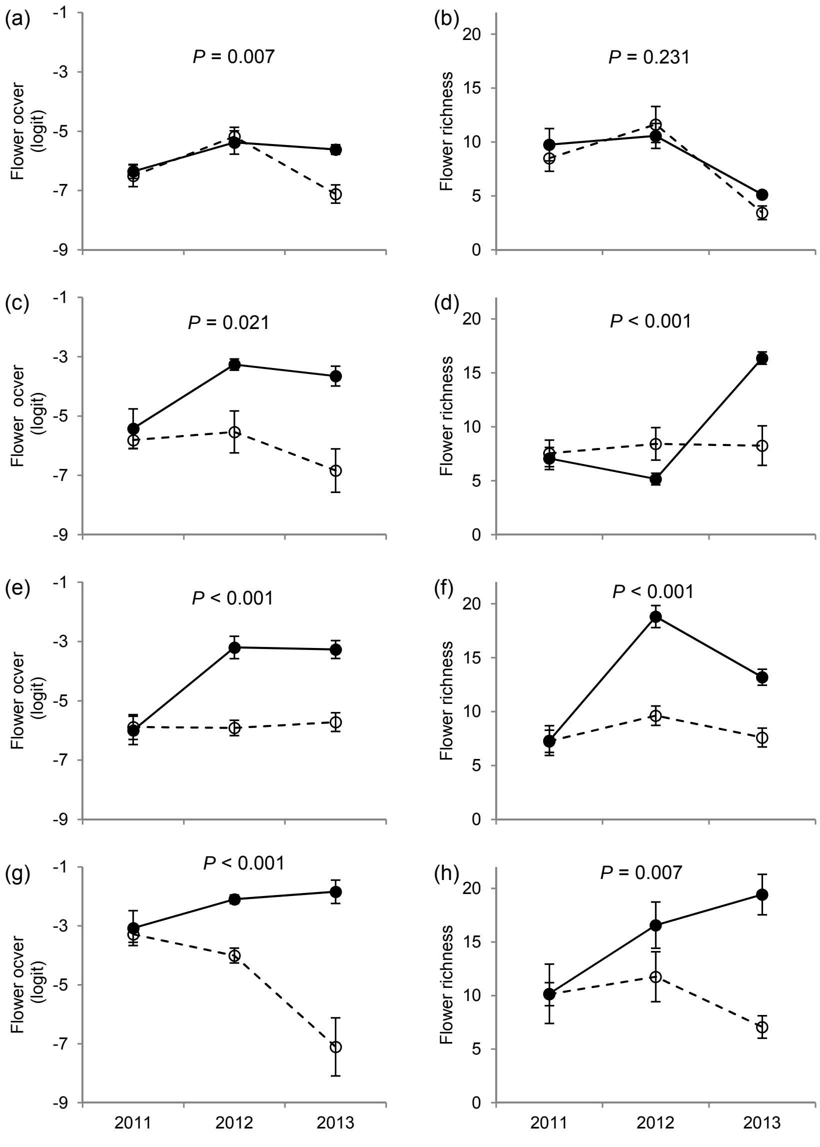

Figure S1. Mean flower cover and species richness in wildflower strips (filled circles, solid lines) and control field boundaries (open circles, dashed lines) in Germany (a, b), Sweden (c, d), The Netherlands (e, f) and the UK (g, h). Error bars represent SE. *P*-values indicate significance of treatment × year interactions (see Table 2).

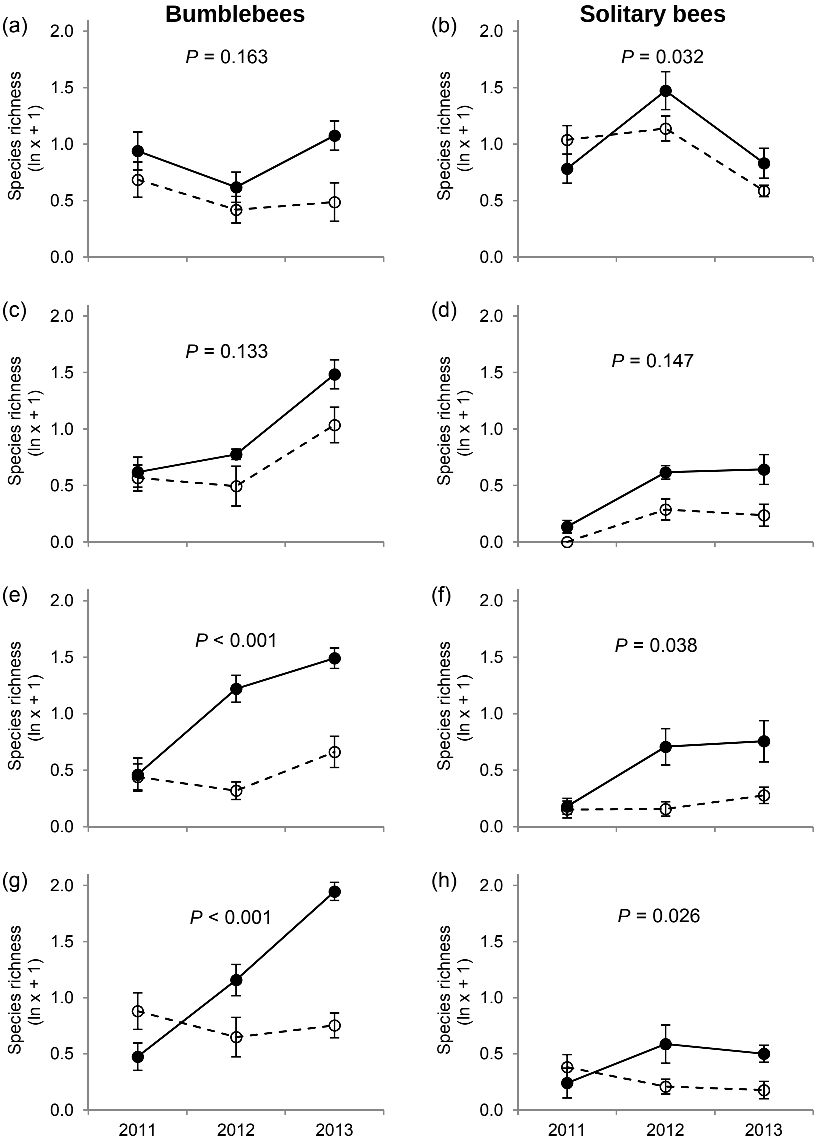

Figure S2. Mean species richness of bumblebees and solitary bees in wildflower strips (filled circles, solid lines) and control field boundaries (open circles, dashed lines) in Germany (a, b), Sweden (c, d), The Netherlands (e, f) and the UK (g, h). Error bars represent SE. *P*-values indicate significance of treatment × year interactions (see Table 2).

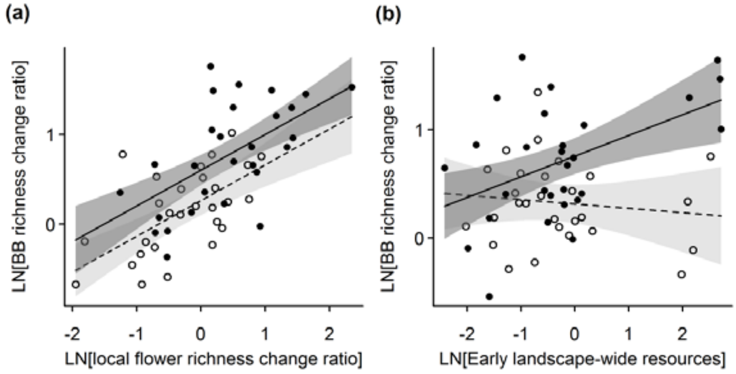

Figure S3. Conditional partial regression plots for the best model explaining the relative change in bumblebee (BB) richness between 2011 and 2013 (see Table 3): (a) effects of local relative change in flower richness between 2011 and 2013, and (b) interacting effects of treatment (wildflower strips, filled circles and solid lines; control field boundaries, open circles and dashed lines) and landscape-wide floral resource availability in May on relative change in bumblebee richness. Plotted points are partial residuals; shaded areas indicate 95% confidence intervals.

CHAPTER 6

Do wildflower strips enhance populations of trap-nesting bees?

Photo: Tibor Bukovinsky

Jeroen Scheper[1], Riccardo Bommarco[2], Maj Rundlöf[3],
Henrik G. Smith[3] & David Kleijn[1,4]

[1]Alterra, Animal Ecology Team, 6700 AA Wageningen, The Netherlands; [2]Swedish University of Agricultural Sciences, Department of Ecology, 750 07 Uppsala, Sweden; [3]Lund University, Department of Biology & Centre of Environmental and Climate Research, 223 62 Lund, Sweden; [4]Wageningen University, Resource Ecology Group, 6700 AA Wageningen, The Netherlands

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Abstract

Evidence for bee declines has increased the need for effective measures mitigating bee loss. Measures that enhance floral resource availability generally increase local richness and abundance of foraging bees, but it remains unclear whether these effects translate into actual enhancement of bee populations. We used trap nests and a three-year Before-After-Control-Impact design to examine whether establishment of wildflower strips enhances local brood cell production of cavity-nesting bee species. We did not find clear evidence for population effects of wildflower strips: wildflower strips enhanced reproduction of *Osmia* spp. compared to control sites, but only in the second year after establishment, and reproduction of none of the other species was significantly affected by wildflower strips. However, the enhancement of nest site availability in wildflower strips and control sites resulted in population growth for all species groups except *Megachile* spp., with for *Osmia* spp. and *Heriades truncorum* relative growth rates increasing with increasing proportion of forest in the surrounding landscape. This probably suggests that most of the investigated species groups are more limited by nest site availability than floral resource availability in agricultural landscapes. Our trap-nest study shows that the large effect sizes of wildflower strips that are often found in studies that measure foraging responses not necessarily reflect local population increases. Whether wildflower strips enhance populations of specific bee species probably depends on the level of congruence between their host plant preference and the plant species composition of wildflower strips.

Introduction

Reported population declines of pollinating insects such as bees (Biesmeijer *et al.* 2006; Kosior *et al.* 2007; Dupont *et al.* 2011) have increased interest in developing and implementing effective measures mitigation pollinator loss. Since bee declines are mainly attributed to loss of floral resources (Scheper *et al.* 2014), measures that target the enhancement of floral resource availability are probably particularly suited to halt or reverse bee decline. Indeed, recent studies show that measures that improve local floral resource availability, such as sown flower strips, generally increase local bee species richness and abundance compared to conventionally managed control sites (Scheper *et al.* 2013; Scheper *et al.* in review). While these results are promising, it remains unclear whether these local effects translate into landscape-wide effects on bee populations, which, to mitigate bee decline, should be the ultimate objective of implementing the measures.

Population-level responses of bees to the implementation of mitigation measures are however difficult to assess. The most widely used approach to evaluate the effects of mitigation measures is to compare species richness and abundance of bees foraging in sites with and without measures (Scheper *et al.* 2013). However, as mobile species with maximum foraging ranges of at least several hundred meters (Knight *et al.* 2005; Zurbuchen *et al.* 2010), bees can readily redistribute themselves over the landscape in response to local pulses of high resources. Implementation of mitigation measures may thereby result in bees being drawn away from lower quality patches and aggregate on the introduced flower-rich patches (Veddeler, Klein & Tscharntke 2006; Bartomeus & Winfree 2011), especially in landscapes that provide few alternative flower resources (Winfree 2010; Scheper *et al.* in review). From these spatio-temporal behavioural foraging responses it cannot be concluded that pollinator populations have increased at sites with mitigation measures.

Assessment of population level effects of mitigation measures would be possible if variables directly related to bee population growth are measured, for instance by using trap nests. Trap nests are artificial nesting sites that can be used to monitor reproduction and population growth of cavity-nesting bee species (Steffan-Dewenter & Schiele 2008). About

5% of the bee species in North-western Europe are cavity-nesting bees that under natural conditions nest in hollow or pithy stems or in cavities in dead wood (Gathmann 1998; Peeters & Nieuwenhuisen 2012). Previous studies have examined effects of conservation measures on reproductive output of bees using trap nests (Gathmann, Greiler & Tscharntke 1994; Kruess & Tscharntke 2002; Albrecht *et al.* 2007; Holzschuh, Steffan-Dewenter & Tscharntke 2010), but because these studies covered single years they were still unable to distinguish population responses from concentration responses. For instance, increased numbers of brood cells in trap nests at mitigation sites may result from enhanced reproduction due to enhanced floral resources, or may alternatively result from more nest-seeking bees being attracted to the more flower-rich mitigation sites (Suzuki *et al.* 2009; Holzschuh *et al.* 2010).

Monitoring reproduction in trap nests over multiple years, in mitigation and control sites located in spatially independent landscapes, and including measurement of base-line brood cell production before the implementation of mitigation measures (i.e. a landscape scale replicated Before-After-Control-Impact (BACI) study design), would allow the detection of bee population responses to establishment of measures such as wildflower strips. Interpretation of the results of such a study is however complicated by the fact that, in addition to the experimental manipulation of flower resources, the placement of trap nests also manipulates nest site availability. The placement of trap nests and the establishment of wildflower strips may therefore lead to a variety of response scenarios:

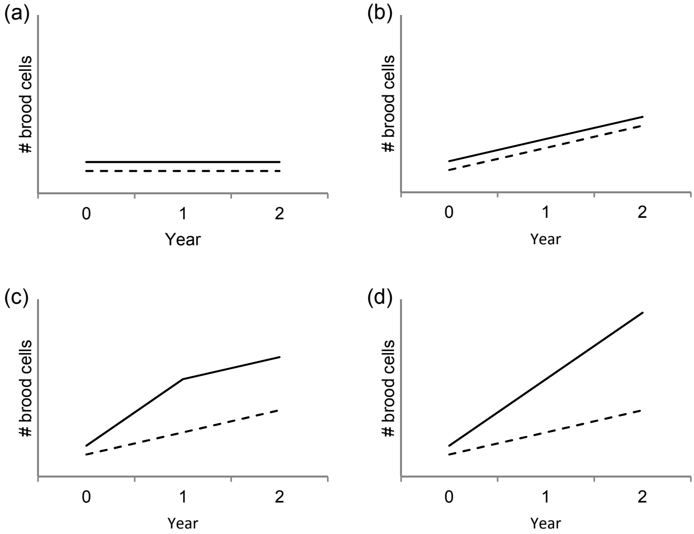

Figure 1. Hypothetical scenarios for the effects of the placement of trap nests and the establishment of wildflower strips on the number of bee brood cells in trap nests. Solid lines: wildflower strips; dashed lines: control sites. Year 0 is the base-line year, prior to establishment of wildflower strips. a) No effects of augmentation of nesting sites or establishment of wildflower strips on the number of brood cells in trap nests. b) A positive effect of enhanced nesting sites only. Brood cell abundance increases similarly in wildflower strips and control sites. c) A positive effect of enhanced nesting sites and a positive effect of wildflower strips on the number of brood cells, but only in the first year after establishment. Brood cell abundance increases more strongly in wildflower strips than in control sites in the first year after establishment, but the increase is similar in the second year. d) Continued positive effects of nest site augmentation and establishment of wildflower strips. Brood cell abundance increases more strongly in wildflower strips than in control sites in the first year and continues to increase more strongly in the second year after establishment.

A) Brood cell densities of trap-nesting bees do not change significantly over the years in either treatment or control sites (Fig. 1a). This suggests that neither the placement of nesting sites nor the establishment of wildflower strips enhances bee brood cell abundance in trap nests. Such a lack of response may indicate that the availability of floral resources and nesting sites in the landscape are not limiting bee populations. Alternatively, this may indicate that floral resources are limiting (Strickler, Scott & Fischer 1996), but that the quantity or quality (e.g. the presence of preferred host plants) of the wildflower strips is insufficient to improve resource availability, and thereby insufficient to attract bees or enhance their reproduction.

B) Bee brood cells increase similarly in treatment and control sites (Fig. 1b), indicating that adding nesting sites enhances brood cell abundance in wildflower strips and control sites to the same extent. This would indicate that nesting sites are limiting bee population growth (Steffan-Dewenter & Schiele 2008; Yamamoto *et al.* 2014). The identical response of bees in wildflower strips and control sites suggests that either floral resource availability is not limiting, or resource availability is not significantly improved by the wildflower strips.

C) Brood cell abundance increases more strongly in wildflower strips than in control sites, but only in the first year after establishment of the strips (Fig. 1c). This may suggest that the increased food supply in the wildflower strips boosted the reproduction of bees in the first year after establishment, but was insufficient to further increase the production of brood cells compared to control sites in the second year. Alternatively, this response may merely indicate a concentration effect of wildflower strips, in which the higher number of brood cells in the wildflower strips results from increased colonization of nests by bees being attracted from the surrounding landscape to the resource-rich strips (Holzschuh *et al.* 2010).

D) Also after the first year, brood cell abundance continues to increase more strongly in wildflower strips than in control sites (Fig. 1d). Such a response cannot be explained by a concentration effect only, and would therefore indicate that the enhanced floral resources provided by the wildflower strips increased reproductive output of bees, and thereby suggests population-level effects of wildflower strips.

In this study, we use trap nests to evaluate the response of cavity-nesting bees to sown wildflower strips. We established wildflower strips along field boundaries in agricultural landscapes in the Netherlands and Sweden. Using a three-year BACI approach, we monitored reproductive output and population dynamics of trap-nesting bees in wildflower strips and control sites, and test whether wildflower strips enhance their reproduction and thus population size. This would be indicated by a response resembling scenario D (Fig. 1d). Furthermore, foraging responses of bees to wildflower strips are affected by the interplay of the level of enhancement of local floral resource availability in the strips and floral resource availability in the surrounding landscape (Scheper *et al.* in review). Likewise, the observed response of bees to placement of artificial nesting sites and establishment of wildflower strips may be expected to depend on the availability of nesting and food resources in the surrounding landscape, and on the extent to which wildflower strips improve local floral resource availability. We therefore additionally test whether variation in bee responses among landscapes depends on environmental factors such as nest site availability and local and landscape level floral resources.

Material and methods

Experimental design

The trap nest experiment was conducted from 2011 to 2013 in Sweden and The Netherlands. In each country, sixteen field boundaries were selected that were adjacent to conventionally managed arable fields. Field boundaries were at least 1 m wide, had a minimum total area of 300 m^2, were dominated by grasses and were generally mown one to three times a year. Each study site was separated by at least 2 km from the nearest neighbouring study site, thereby ensuring spatial independence among sites (Zurbuchen *et al.* 2010). Half the sites in each country were designated as “mitigation” sites. Here, at the end of first study year, wildflower strips were established alongside the field boundaries (hereafter referred to as “pre-treatment field boundaries”). The other sites were used as control field boundaries. Care was taken to ensure that landscapes surrounding the mitigation and control sites covered similar gradients in proportion of semi-natural habitat, proportion of forest, land use intensity, and landscape-wide floral resource availability (Table S1).

Wildflower strips were established in mitigation sites in autumn 2011. Strips of 3 × 100 m were sown alongside field boundaries using a seed mixture (2 g m^{-2}) of mid- to late-season flowering plants attractive to bees, 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%). Flower strips were not fertilized or managed during the two years after their establishment.

Monitoring population dynamics in trap nests

At each wildflower strip and control field boundary we placed three trap nests, spaced at least 10 m apart. Trap nests were composed of two plastic tubes (Sweden: ø 7 cm, 17 cm long; The Netherlands: ø 11 cm, 20 cm long), filled with internodes of common reed *Phragmites australis* (ø 2-12 mm), mounted on a 1.5 m wooden pole. In Sweden insufficient large diameter reed internodes (ø 6-12 mm) were available and reed internodes were therefore supplemented with paper tubes (ø 6-10 mm). In the Netherlands, trap nests were placed in the field from late-March to mid-September, with the exception of 2011 when trap nests were set up late-April. In Sweden, trap nests were exposed from early-May to mid-September. Trap nests collected in September were stored at temperatures resembling outside temperatures to enable larvae to complete development before hibernation. After six weeks, trap nests were moved and stored in a cooling chamber at 2-6°C to mimic hibernation conditions.

During the winter, reed internodes colonized by bees were taken out of the cylinders and carefully dissected using a scalpel. All brood cells located between the opening and the node of a reed stem were classified as belonging to one brood nest (Steffan-Dewenter & Schiele 2008); nests that were built on both sides of the node were considered as two different nests. We identified the brood cells of each brood nest to the lowest possible taxonomic level based on the characteristics of the larvae or cocoon, cell wall material and food remains. Based on these characteristics, *Heriades truncorum* was identified to species, whereas *Hylaeus* spp., *Osmia* spp. and *Megachile* spp. could only be identified to genus. For each nest we recorded the total number of brood cells, the number of viable cells and the number of dead brood cells, either killed by cleptoparasites and parasitoids or unknown other causes. Any encountered mites were removed and killed using ethanol to avoid mites colonizing any of the other trap nests in storage. After examination of the brood cells, the reed internodes were closed with tape and stored in a cooling chamber.

To monitor population dynamics, occupied reed internodes were returned to field the following spring, allowing bees to emerge at their original mitigation or control site. Occupied nests were placed in emergence tubes (ø 6 cm; 26 cm long) covered with wire mesh (0.7 cm mesh width). These tubes were longer than the internodes to prevent emerging bees to make new nest in the old internodes. The emergence tubes were fit to the original poles from which the nests were removed the previous year. Each pole was again equipped with a set of trap nests, in which the occupied internodes were replaced by empty new internodes. In addition, to ensure that local nest site availability did not limit population growth, we fitted additional trap nests to poles at sites with high numbers of colonized of internodes. For every 30 occupied internodes per trap nest, we added one extra trap nest to the pole. The procedure described above was repeated each year from 2011 to 2013.

Quantifying availability of flower resources and nesting sites

We measured local species richness of flowering forbs and total percentage cover of all flowering forbs in wildflower strips and control field boundaries by surveying two transects of 150 m^2. Dimensions of the transects varied among sites, but had a minimum width of 1 m and a maximum width of 3 m. Each year, surveys were carried out four times per year: twice before peak-flowering of the sown species in the wildflower strips (The Netherlands: April - May; Sweden: May - June) and twice during peak-flowering (June - August). Regarding the mitigation sites, baseline data on local flower resources was collected in pre-treatment field boundaries in 2011, whereas in 2012 and 2013 surveys were carried out in the established wildflower strips.

Landscape-wide floral resource availability in study landscapes, defined as the area in a 1 km radius around study sites, was quantified using a stratified sampling approach. We estimated early- (The Netherlands: May; Sweden: June) and late-season (July – August) landscape-wide floral resource availability (see Scheper *et al.* in review for further details). These direct measures of floral resource availability have been shown to better predict bee responses in the study system than proxies for floral resource availability, such as land use intensity or proportion of semi-natural habitat (Scheper *et al.* in review).

Given the importance of woody habitats as nesting sites for cavity-nesting bees, we used the proportion of forest in study landscapes as proxy for the availability of nesting sites (Fabian *et al.* 2013; Hudewenz & Klein 2013). The proportion of forest cover (including wooded banks and hedgerows) in study landscapes was determined using national topographical maps and aerial photographs, validated by field inspections.

Statistical analyses

All analyses were performed using R version 3.1.0 (R Core Team 2014). Inferences about population-level effects of wildflower strips should ideally be made at the level of individual bee species, because pooled bee responses may mask differential responses of different bee species. We therefore analysed the effects of wildflower strips at the lowest possible taxonomic level, and performed separate analyses for *Osmia* spp., *Heriades truncorum*, *Hylaeus* spp. and *Megachile* spp. Low number of observations prevented analysis of effects on *Chelostoma* spp. The studied *Osmia* species (predominantly *Osmia bicornis*) are active early in the season (April-May), mainly before peak-flowering of the sown plant species in the wildflower strips, whereas the other bee taxa are active mid- to late-season (June-August), during peak flowering of the wildflower strips.

One Dutch mitigation site was omitted from all analyses because the trap nests had been vandalized in 2012 and 2013. The 2013 data from another Dutch mitigation site was excluded from the analyses of late-emerging bee, because the trap nests were overgrown with tall weeds (*Urtica dioica*, *Convolvulus sepium*) and were inaccessible to nest-seeking bees from June onwards. In Sweden, at each of three sites two trap nests (i.e. one pole) was destroyed in 2012 and results for these sites were based on the average of the remaining nests. In the Netherlands, trap nests were deployed in the field later in the season (April) in 2011 than in 2012 and 2013 (March) but this did not affect the significance of results for early-emerging bees: similar results were produced when the 2011 data from the Netherlands were excluded from the analyses.

We used linear mixed models, with brood cell abundance summed over all trap nests per site as response variable, to examine the effects of wildflower strip establishment on the different cavity-nesting bee species groups. We analysed effects on total brood cell abundance as well as effects on abundance of viable brood cells, i.e. brood cells not killed by natural enemies or other causes. Analyses were performed on ln (x + 1) transformed data to improve normality and homoscedasticity of residuals. These models had better diagnostic plots for normality of errors and homogeneity of variance than generalized linear mixed models with Poisson or negative binomial distributions on untransformed data. Linear mixed models included the fixed factors treatment (control vs. pre-treatment or sown flower strip), year and their interaction. Effects of wildflower strips on brood cell abundance would be indicated by a significant treatment × year interaction, assessed by backward model simplification and likelihood ratio tests with Maximum Likelihood. We used non-orthogonal contrasts to decompose significant treatment × year interactions into separate 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 (Fig. 1d) and would be indicative of population-level effects. Linear mixed models included country as random factor, allowing the intercept and/or slope to vary between countries, because we were interested in the overall effects of wildflower strips on brood cell production rather than in country-specific patterns. Models for effects on total and viable brood cell abundance of *Osmia* spp. included country and study site nested within country as random factors, with random slopes defined by year, to account for the hierarchical structure and repeated measures in the design. Models for effects on the other bee species groups included random intercepts only, as these provided better fit to the data (as indicated by likelihood ratio tests) than models including both random intercepts and slopes. We used similar approaches to analyse the effects of sown wildflower strips on local floral resource availability, measured as flower cover (logit transformed) and richness, during peak activity of the early- and late-emerging bee species.

Next, we investigated whether and to what extent variation in effects of wildflower strips within species groups can be explained by the level of improvement of local floral resources in the strips and the availability of nesting and food resources in the surrounding landscape. In these analyses we used the relative growth in brood cell abundance in mitigation and control sites between 2011 and 2013 as response variable, measured as the log response ratio ($\ln \frac{X+1_{2013}}{X+1_{2011}}$). Likewise, changes in local floral resource availability were measured as the relative change (ln response ratio) in flower cover and richness in mitigation and control sites between 2011 and 2013. The explanatory variables early-season (in May - June) and late-season (in July-August) landscape-wide floral resource availability were ln transformed and percentage cover of forest was ln (x+1) transformed to reduce positive skew.

For the analysis of relative growth of brood cells of the early-emerging *Osmia* spp. we constructed a model set consisting of all possible combinations of two-way interactions (including main effects) between the explanatory variables treatment, relative change in early-season local flower cover, relative change in early-season local flower richness, early-season landscape-wide floral resource availability, and forest cover. We also included models composed of the additive main effects for each possible pair of explanatory variables, as well as models composed of the single main effect of each explanatory variable. An intercept only model was included for reference. To avoid problems with overfitting we did not examine higher order interactions. These analyses were performed using linear mixed models, with country as random factor. A similar approach was used to analyse the responses of the late-emerging bee species, except that this analysis included late- instead of early-season local and landscape floral resource variables.

We used an information-theoretic approach to assess the relative support for the different models in the model set. Models were ranked based on their Akaike information criterion values corrected for small sample size (AIC_c). We restricted our candidate set to models with Δ $AIC_c < 2$ (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.

Results

Over the three year study period, a total of 2,642 reed internodes were colonized by *Osmia* spp., producing a total of 11,992 brood cells. Of these, 9,026 brood cells were intact, 701 were killed by natural enemies and 2,265 were killed by other causes. The late-emerging bee species colonized 1,971 nests and produced 8,932 brood cells, with 7,583 cells intact, 162 killed by natural enemies and 1,187 killed by other causes. *Megachile* spp. (40.3%) accounted for the majority of the brood cells produced by late-emerging bee species, followed by *Hylaeus* spp. (34.7%) and *Heriades truncorum* (23.4%). Only 1.5% of the brood cells of late-emerging bee species were produced by *Chelostoma* spp.

Effects of wildflower strips on bee brood cell abundance

Sown wildflower strips did not improve local early-season floral cover (treatment × year interaction: $\chi^2_{(2)} = 1.50$, $P = 0.473$, Fig. S1a). After establishment, flower richness appeared to be higher in wildflower strips than in control sites, but this effect was not significant ($\chi^2_{(2)} = 2.02$, $P = 0.363$, Fig. S1b). Nevertheless, establishment of wildflower strips significantly enhanced *Osmia* spp. brood cell abundance in wildflower strips compared to control sites, with similar patterns for viable and total brood cells (Table 1). In both wildflower strips and control sites, brood cell abundance increased over the years, but the increase was stronger in wildflower strips (Fig. 2a, Fig. S2a). Contrasts revealed that the stronger increase in wildflower strips only became apparent in the second year after establishment of the strips (contrast for treatment × $\text{year}_{2012 \text{ vs. } 2013}$ viable cells: $t_{(58)} = 2.12$, $P = 0.038$; total cells: $t_{(58)} = 1.90$, $P = 0.063$); in the first year after establishment increases were similar in wildflower strips and control sites (contrast for treatment × $\text{year}_{2011 \text{ vs. } 2012}$ viable cells: $t_{(58)} = -0.43$, $P = 0.666$; total cells: $t_{(58)} = -0.64$, $P = 0.526$).

Table 1. Results of linear mixed models for interaction effects of treatment (wildflower strip vs. controls site) and year on viable and total bee brood cell abundance. Significant treatment × year interactions are shown in bold.

	Viable cells		Total cells	
	χ^2	P	χ^2	P
Early-emerging bees				
Osmia spp.	6.48	**0.039**	6.40	**0.041**
Late-emerging bees				
Heriades truncorum	2.77	0.251	2.54	0.280
Hylaeus spp.	1.06	0.587	0.74	0.690
Megachile spp.	3.17	0.205	2.84	0.242

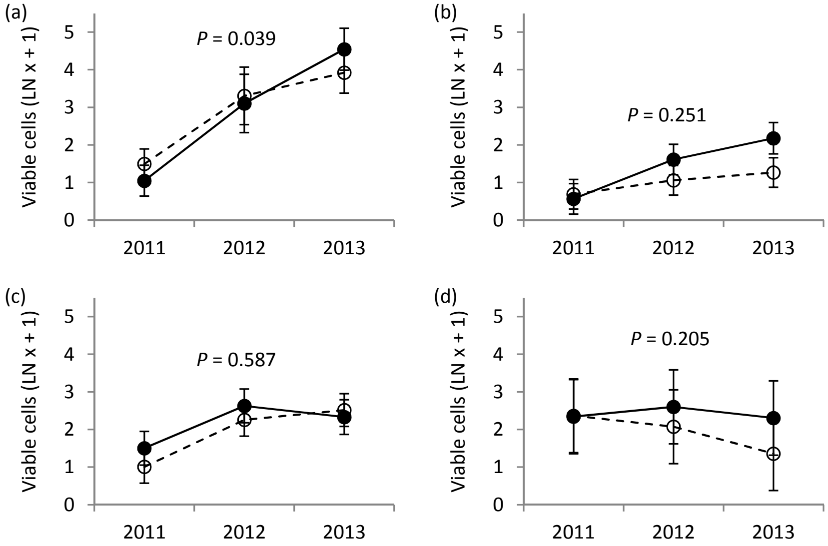

Figure 2. Mean viable brood cell abundance of early-emerging *Osmia* spp. (a) and late-emerging *Heriades truncorum* (b), *Hylaeus* spp. (c) and *Megachile* spp. (d) in wildflower strips (filled circles, solid lines) and control field boundaries (open circles, dashed lines). Error bars represent model estimated SE. *P*-values indicate significance of treatment × year interactions.

Local late-season flower cover and richness were significantly enhanced by wildflower strips establishment compared to control sites (treatment × year interaction flower cover: $\chi^2_{(2)} = 20.41$, $P < 0.001$; flower richness: $\chi^2_{(2)} = 11.55$, $P = 0.003$). Wildflower strips resulted in enhanced flower cover in 2012 (contrast for treatment × $\text{year}_{2011 \text{ vs. } 2012}$: $t_{(57)} = -3.91$, $P < 0.001$) after which the difference between wildflower strips and control sites remained constant in 2013 (contrast for treatment × $\text{year}_{2012 \text{ vs. } 2013}$: $t_{(57)} = 0.40$, $P = 0.691$; Fig. S1c). Flower richness was also increased in flower strips, but only significantly from 2012 to 2013 (contrast for treatment × $\text{year}_{2011 \text{ vs. } 2012}$: $t_{(57)} = -1.27$, $P = 0.208$; treatment × $\text{year}_{2012 \text{ vs. } 2013}$: $t_{(57)} = 2.15$, $P = 0.036$; Fig. S1d). Despite the positive effects of wildflower strips on local late-season flower cover and richness, brood cell abundance of the late-emerging bee species was not significantly enhanced by wildflower strips (Table 1), although for *Heriades truncorum* and *Megachile* spp. diverging trends in wildflower strips and control sites were observed (Fig. 2b,d; Fig. S2b,d). In general, brood cell abundance of *Heriades truncorum* (effect of year for viable cells: $\chi^2_{(2)} = 10.53$, $P = 0.005$; total cells: $\chi^2_{(2)} = 8.45$, $P = 0.015$) and *Hylaeus* spp. (viable cells: $\chi^2_{(2)} = 13.73$, $P = 0.001$; total cells: $\chi^2_{(2)} = 17.88$, $P < 0.001$) increased over the years in wildflower strips and control sites. However, while brood cell abundance of *Heriades truncorum* continued to increase over the course of the study (Fig. 2b, Fig. S2b), the increase in brood cells of *Hylaeus* spp. levelled off in 2013 (Fig. 2c, Fig. S2c). No significant effect of year was observed for brood cell abundance of *Megachile* spp. (viable cells: $\chi^2_{(2)} = 4.86$, $P = 0.088$, Fig. 2d; total cells: $\chi^2_{(2)} = 5.85$, $P = 0.054$, Fig. S2d).

Although not specifically tested, the consistency of total and viable brood in all investigated taxa suggests that the differential effects of wildflower strips across taxa are not caused by different effects on mortality rates of brood cells.

Factors affecting bee responses

Model selection based on AIC$_c$ revealed that the variation in relative growth of intact brood cells of *Osmia* spp. between 2011 and 2013 was best explained by the model including the effects of treatment and the proportion of forest in the surrounding landscape ($\omega = 0.44$, Table 2). This model indicates that, in addition to the positive effect of wildflower strips on the relative growth in viable brood cells, the level of growth increased with increasing proportion of forest. Although there was considerable model selection uncertainty, all competing models in the candidate set included treatment and/or forest cover (Table 2). The best model performed better than the more complex second-best model, and was 1.6 times more likely to be the best model than the more parsimonious model that included forest cover only. Similar results were observed for the total abundance of brood cells, but with relative weaker support for the best model ($\omega = 0.37$; Table S2).

The proportion of forest also explained the variation in the relative increase in brood cell abundance of *Heriades truncorum*. The highest ranked model in the candidate set suggests that the relative growth of viable brood cells increased with increasing proportion of forest ($\omega = 0.44$). The other, more complex models in the candidate also included the positive effect of forest cover (Table 2). Results for relative growth of total number of brood cells resembled those for viable brood cells, with the best model only including a positive effect of forest cover ($\omega = 0.37$). However, the support for the effect of forest cover was less clear, as the candidate set for total brood cells also included models not containing forest cover (Table S2).

Table 2. Candidate models (Δ AIC$_c < 2$) explaining the relative growth in viable bee brood cell abundance in wildflower strips and control sites between 2011 and 2013. Models are ranked in order of increasing differences in corrected Akaike information criterion (Δ AICc). Models ranked lower than the intercept-only model are not shown. Regression coefficients, standardized by centring and dividing by 2 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. INT = intercept, TR = treatment (wildflower strip vs. controls site), FOR = proportion forest cover, COV$_{Late}$ = relative change in late-season local flower cover between 2011 and 2013.

	Explanatory variable					**DF**	**AIC$_c$**	**Δ AIC$_c$**	**ω**
	INT	TR	FOR	TR × FOR	COV$_{Late}$				
Early-emerging bees									
Osmia spp.									
model 1	2.92	0.99	1.59			5	119.4	0.00	0.44
model 2	2.93	0.99	1.75	-1.49		6	120.3	0.84	0.29
model 3	2.92		1.61			4	120.4	0.98	0.27
Late-emerging bees									
Heriades truncorum									
model 1	0.94		2.26			4	114.8	0.00	0.44
model 2	0.94	0.73	2.13			5	115.1	0.34	0.37
model 3	0.94		2.18		0.54	5	116.4	1.58	0.20
Hylaeus spp.									
model 1	1.18					3	142.8	0.00	0.27
Megachile spp.									
model 1	-0.52	1.04				4	122.0	0.00	0.38
model 2	-0.52					3	122.36	0.41	0.31

None of the explanatory variables in the analyses explained the variation in total brood cell growth for *Hylaeus* spp. and *Megachile* spp.: for both species groups the intercept-only model was the highest ranked model (Table S2). For *Hylaeus* spp. the intercept-only model was also the highest ranked model for growth in intact brood cells (Table 2). Variation in growth of viable brood cells of *Megachile* spp. was best explained by the model including the effect of treatment, but this model hardly performed better than the intercept-only model (Δ $AIC_c = 0.41$).

Discussion

While wildflower strips generally have large, positive effects on local densities of foraging bees (Scheper *et al.* 2013; Scheper *et al.* in review), our trap-nest study shows that these effects not necessarily reflect local population increases. We did not detect clear population effects of wildflower strips, as would be indicated by continued enhanced reproduction (response scenario D, Fig. 1d), for any of the examined trap-nesting bee taxa. The response of *Osmia* spp. did resemble scenario D, but the effects were moderate and only became apparent in the second year after establishment of the wildflower strips (Fig. 2a, Fig. S2a). None of the other species was significantly affected by wildflower strip establishment, despite a positive trend for the effects of wildflower strips on brood cell production of *Heriades truncorum* and *Megachile* spp. However, enhancing nest site availability through placement of artificial trap nests appeared to generally increase bee populations in wildflower strip and control sites, as brood cell abundance of all taxa, except *Megachile* spp., steadily increased over the years (Fig. 2, Fig. S2). For *Osmia* spp. and *Heriades truncorum*, the level of growth in brood cells increased with the proportion of forest cover in the surrounding landscape (Table 2, Table S2).

The discrepancy between the results of the current trap nest study and the generally clear positive effects of wildflower strips on forager densities in previous studies (Scheper *et al.* 2013), including a transect-walk study conducted in the same sites as the present study (Scheper *et al.* in review), highlights the fundamental difference between evaluating the effectiveness of wildflower strips based on measurements of foraging or reproduction responses. Bees may either use wildflower strips to forage for nectar (for energy) or pollen (source of protein and minerals), with the latter being the essential food source required to rear offspring. All bees, both male and female, and both nest-building and cuckoo bees, forage for nectar, but only nest-building female bees collect pollen to provision their brood cells. While individual bee species generally can exploit a wide variety of plant species for nectar, even the most generalist bee species are restricted in their pollen host plant use and often have distinct preferences for specific pollen host plants (Scheper *et al.* 2014). Brood cells provisioned with pollen from less-preferred or non-host plant species may result in lower quality offspring (Tasei & Aupinel 2008) or no offspring production at all (Sedivy, Müller & Dorn 2011). Consequently, while both males and females of a wide variety of bee species may be attracted from the surrounding landscape to forage for nectar in wildflower strips, and thus lead to large effects in terms of forager densities, effects on reproduction depend on the plant species composition of the wildflower strips and the specific pollen host plant preferences of bee species. Positive effects of wildflower strips on bee populations may therefore be expected to be restricted to the bee species whose preferred pollen host plant species are present in the strips. Furthermore, even if the wildflower strips contain the right host plants for a particular bee species, impacts on its reproduction requires a sufficient amount of the host plants to meet the species' quantitative pollen requirements (Müller *et al.* 2006).

Following on from this, the observed differential responses of the investigated trap-nesting bee taxa to the wildflower strips can be explained by the level of conformance between bees' pollen host plant preference and the plant species composition of the wildflower strips. For instance, the total lack of effects of wildflower strips on populations of *Hylaeus* spp. (Fig 2c), despite the enhanced flower cover and richness (Fig. S1c,d), likely reflects that plant species preferred by most *Hylaeus* species, such as *Rubus* spp., *Cirsium arvense* and *Jasione montana* (Raemakers 2012), were not present or scarce in the strips (data not shown). Likewise, although the seed mix used to establish wildflower strips included preferred host plants of *Heriades truncorum* (Asteraceae; Peeters 2012) and common *Megachile* species (Asteraceae and Fabaceae; Nieuwenhuizen 2012; J. Scheper unpublished data), the quantities of these plant species in the relatively small-sized strips (300 m^2) was probably insufficient to produce measurable effects on the reproduction of these bee species. In contrast, reproduction of *Osmia* spp., predominantly the common, highly generalist species *Osmia bicornis*, was positively affected by wildflower strips (Fig. 2a). This may seem surprising, given that wildflower strip establishment did not significantly enhance early-season flower cover and richness (Fig. S1a,b), but probably reflects differences in species composition between wildflower strips and control field boundaries, with flower strips containing more spontaneously established *Ranunculus* spp., Brassicacea and sown *Trifolium* spp. (data not shown) that are preferred by *O. bicornis* (Sedivy, Müller & Dorn 2011; J. Scheper unpublished data). In addition, the activity period of *O. bicornis* extends beyond May, and populations may have partly profited from higher flower cover and richness in wildflower strips in early- to mid-June. The positive effects of wildflower strips on population growth of *O. bicornis* would nevertheless probably have been more pronounced if early-flowering host plant species had been included in the seed mixture.

While effects of wildflower strips were restricted to *Osmia* spp., all taxa except the *Megachile* species appeared to be positively affected by the experimental enhancement of nest site availability in the agricultural landscapes, as indicated by the general increase in brood cell production in trap nests over the years (Fig. 2, Fig. S2). The deviating results for *Megachile* spp., which resemble response scenario A (Fig. 1a), may imply that these species, many of which also nest below-ground (Nieuwenhuizen 2012), were less limited by nest site availability, or may point to negative effects of competition with the high performing earlier emerging *Osmia* spp., which prefer the same nest entrance diameters as those preferred by the *Megachile* species. Alternatively, populations of *Megachile* species may have been more limited by insufficient availability of pollen host plants in the agricultural landscapes. We cannot with certainty ascribe the enhanced reproduction of the other bee taxa to the placement of trap nests, as assessing whether adding trap nests increases bee population sizes would require comparing bee population sizes in sites with and without trap nests, with population size estimated independently by other methods (Roulston & Goodell 2011). The observed population growth might as well have resulted from random changes in environmental conditions, such as for instance improved weather conditions during the three-year period. However, other studies performed in agricultural systems, including studies using additional sampling methods (Stubbs, Drummond & Allard 1997; Yamamoto *et al.* 2014), have reported similar population increases after introduction of experimental trap nests (Strickler, Scott & Fischer 1996; Sheffield *et al.* 2008; Steffan-Dewenter & Schiele 2008;), providing support for the positive effect of augmenting nesting sites on populations of cavity-nesting bees in agricultural landscapes.

Of the species that displayed population growth, the level of growth of *Osmia* spp. and *Heriades truncorum* increased with the proportion of forest cover in the surrounding landscape, whereas *Hylaeus* spp. did not (Table 2, Table S2). Colonization of trap nests has been shown to increase with increasing cover of forest (Fabian *et al.* 2013; Hudewenz &

Klein 2013, but see Schüepp *et al.* 2011), probably because the availability of nesting sites in these woody habitats support source populations of cavity-nesting bees that colonize the trap nests. However, regarding effects on relative growth rates, the inconsistent effects of the proportion of forest for *Osmia* spp. and *Heriades truncorum* on the one hand and *Hylaeus* spp. on the other, may suggests that the effects of forest cover are driven by other mechanisms than nest site availability. For *Osmia bicornis*, *Acer* spp. (J. Scheper unpublished data) and *Quercus* spp. (Raw 1974) provide suitable pollen resources in forests, whereas for *Heriades truncorum* forests provide essential nest-building materials in the form of tree resins. We therefore speculate that the positive effects of forest cover on population growth are driven by the provision of food and nest-building resources.

Conclusion

Given that budgets for biodiversity conservation are limited, insight in whether and under what conditions mitigation measures enhance bee populations is essential to allocate funds and efforts to promote bees to their best use. Although the observed patterns for the response of *Osmia* spp., as well as *Heriades truncorum* and *Megachile* spp., may point towards population-level effects, our study did not provide unequivocal evidence for population-level effects of wildflower strips on trap-nesting bees. This may suggest that the size of the strips was too small and/orthe two-year monitoring period too short to detect clear population responses. Nevertheless, the differential responses across taxa suggest that population-level effects of wildflower strips may be expected to be species-specific and likely depend on the match between bees' host plant preference and the plant species composition of the strips. To promote bee populations, design of seed mixes for wildflower strips should therefore be based on clear objectives regarding target species and include the corresponding preferred pollen host plants of target species (Scheper *et al.* 2014).

The generally positive effects of artificial nesting resources on populations of cavity-nesting bees indicate that most of the investigated species groups are currently probably more limited by nest site availability than by floral resource availability in agricultural landscapes. Thus, installing trap nests may in itself be an effective bee conservation measure. In addition, given the important functional role of many megachilid species in the pollination of crops (Bosch & Kemp 2002; Pitts-Singer & Cane 2011), establishing trap nests near crops may be a cost-effective management practice to enhance pollination and crop yield (Artz *et al.* 2013; Garibaldi *et al.* 2014). Still relatively little is known about the extent to which ground-nesting bees, which from the large majority of the bee species in Europe, are limited by nesting sites in contemporary agricultural landscapes and how nest site availability for these species can be enhanced. Further research is required to fill this important knowledge gap currently limiting our ability to promote wild bee populations in agricultural landscapes.

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SUPPORTING INFORMATION

Table S1. Means (± standard errors) and ranges (in parentheses) for nitrogen input in agricultural fields, proportion of semi-natural habitat, proportion of forest and estimated flower cover in landscapes surrounding (1 km radius) wildflower strips and control field boundaries in the four study countries in 2011 – 2013.

	N input (kg^{-1} ha^{-1} $year^{-1}$)	**Semi-natural habitat (%)**	**Forest (%)**	**Flower cover in May (%)**	**Flower cover in July – August (%)**
Sweden					
Control	113.5 ± 9.3 (78.8 – 146.9)	7.8 ± 2.0 (2.9 – 20.6)	3.3 ± 1.1 (0.0 – 8.0)	0.55 ± 0.08 (0.18 – 0.99)	0.51 ± 0.05 (0.30 – 0.78)
Flower strip	116.0 ± 8.8 (67.3 – 140.9)	8.8 ± 1.6 (2.8 – 13.9)	1.9 ± 0.5 (0.0 – 3.7)	0.66 ± 0.11 (0.19 – 1.16)	0.59 ± 0.07 (0.29 – 1.19)
Netherlands					
Control	215.5 ± 16.0 (158.5 – 279.0)	5.3 ± 0.7 (2.4 – 9.2)	9.8 ± 1.9 (3.0 – 18.3)	0.23 ± 0.03 (0.04 – 0.44)	0.08 ± 0.01 (0.02 – 0.15)
Flower strip	227.7 ± 14.3 (162.0 – 276.8)	7.3 ± 1.3 (2.1 – 13.5)	15.5 ± 3.5 (3.9 – 35.2)	0.39 ± 0.07 (0.08 – 0.83)	0.12 ± 0.02 (0.02 – 0.51)

Table S2. Candidate models (Δ AIC_c < 2) explaining the relative growth in total brood cell abundance in wildflower strips and control sites between 2011 and 2013. Models are ranked in order of increasing differences in corrected Akaike information criterion (Δ AICc). Models ranked lower than the intercept-only model are not shown. Regression coefficients, standardized by centring and dividing by 2 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. INT = intercept, TR = treatment (wildflower strip vs. controls site), FOR = proportion forest cover, COV_{Late} = relative change in late-season local flower cover between 2011 and 2013, RES_{Late} = late-season landscape-wide floral resource availability.

	Explanatory variable						**DF**	**AIC_c**	**Δ AIC_c**	**ω**
	INT	TR	FOR	TR × FOR	COV_{Late}	RES_{Late}				
Early-emerging bees										
Osmia spp.										
model 1	3.04	1.03	1.68				5	121.6	0.00	0.37
model 2	3.05	1.03	1.86	-1.61			6	122.2	0.65	0.26
model 3	3.04		1.71				4	122.6	1.01	0.22
model 4	3.07	1.11					4	123.4	1.80	0.15
Late-emerging bees										
Heriades truncorum										
model 1	0.87		2.36				4	117.7	0.00	0.37
model 2	0.87	0.77	2.22				5	118.0	0.31	0.31
model 3	0.86	2.27			0.60		5	119.2	1.45	0.18
model 4	0.98					1.78	4	119.6	1.86	0.14
Hylaeus spp.										
model 1	1.35						3	142.3	0.00	0.32
Megachile spp.										
model 1	-0.59						3	126.0	0.00	0.24

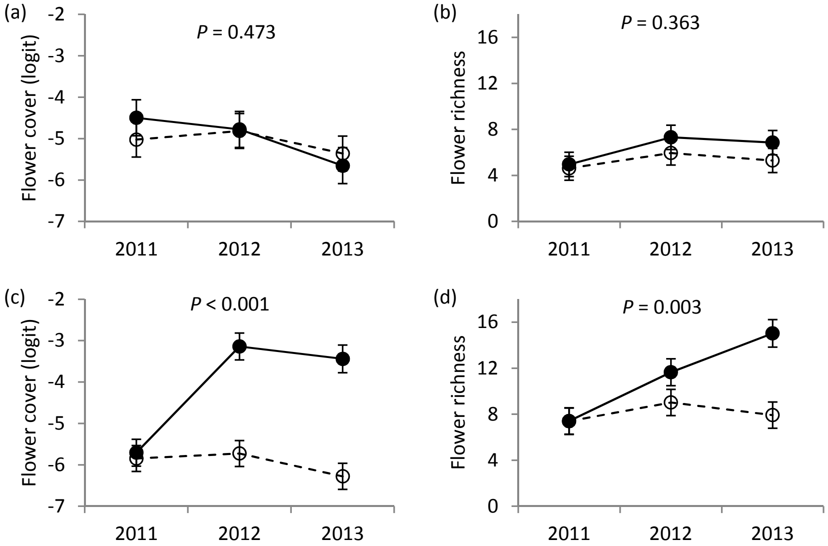

Figure S1. Mean early-season (a, b) and late-season (c, d) flower cover and species richness in wildflower strips (filled circles, solid lines) and control field boundaries (open circles, dashed lines). Error bars represent model estimated SE. *P*-values indicate significance of treatment × year interactions.

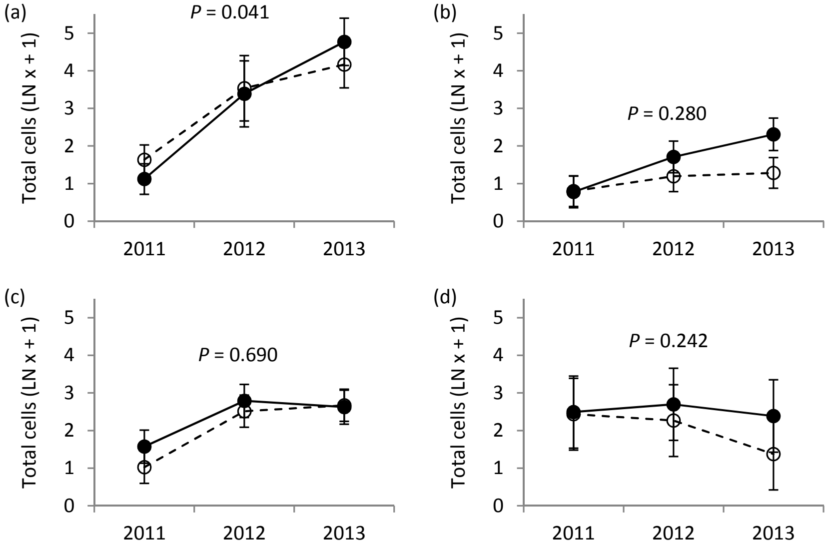

Figure S2. Mean total brood cell abundance of early-emerging *Osmia* spp. (a) and late-emerging *Heriades truncorum* (b), *Hylaeus* spp. (c) and *Megachile* spp. (d) in wildflower strips (filled circles, solid lines) and control field boundaries (open circles, dashed lines). Error bars represent model estimated SE. *P*-values indicate significance of treatment × year interactions.

CHAPTER 7

General discussion

Photo: David Kleijn

Introduction

Widespread and unprecedented rates of loss of biodiversity, attributed to anthropogenic environmental pressures, have raised concern about the imminence of the Earth's 6th mass-extinction event (Barnosky *et al.* 2011). The Convention on Biological Diversity aimed to achieve a substantial reduction of the rate of biodiversity loss by 2010, but general consensus is that this target has not been met (Butchart *et al.* 2010). Among the taxa that are currently under threat, pollinating insects such as wild bees have been the focus of particular concern among researchers and policy makers (Natural Research Council 2007; Potts *et al.* 2010). This is exemplified by the recent decision of the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) to give pollination top priority in their first assessment. Accumulating evidence suggests that many wild bee species have declined in Europe over the last decades (Biesmeijer *et al.* 2006; Kosior *et al.* 2007; Patiny *et al.* 2009; IUCN 2014). This may have, in addition to consequences for intrinsic values of biodiversity, adverse effects on ecosystem functioning and the delivery of ecosystem services (Ollerton *et al.* 2011; Garibaldi *et al.* 2013). Reported bee declines have therefore caused concern about a potential global pollination crisis (Steffan-Dewenter *et al.* 2005; but see Ghazoul 2005) and increased the urgency to identify the drivers of wild bee losses and address these with effective conservation measures.

This thesis aims to establish the main causes of wild bee decline and to evaluate and understand the effectiveness of measures counteracting bee decline in European agricultural landscapes. Specifically, we investigated whether and to what extent wild bee decline is driven by loss of floral resources in contemporary intensively used agricultural landscapes, and how effects of floral resources determine the effectiveness of measures that aim to halt and reverse bee decline. We convincingly linked the decline of wild bee species to the loss of their favoured host plants, and, in both a quantitative review and a cross-country field experiment, demonstrated the importance of the induced ecological contrast in floral resources for the effectiveness of mitigation measures. These insights offer concrete tools for effective management practices that aim to promote wild bees.

This final chapter synthesizes and discusses the results of the different studies presented in the thesis, addresses their implications with respect to wild bee conservation and pollination service delivery, and explores directions for future research.

Drivers of wild bee decline

Land use change and agricultural intensification are considered the most important drivers of wild bee decline (Potts *et al.* 2010; González-Varo *et al.* 2013). It is generally believed that these environmental pressures mainly drive bee decline through loss of floral resources (Carvell *et al.* 2006; Winfree *et al.* 2011), but so far this has been largely based on speculation.

We demonstrated that bee population decline is indeed associated with loss of floral resources (Chapter 2). However, besides their impact on floral resource availability, land use change and agricultural intensification have also affected the availability of nesting sites and exposure to risk factors such as pesticides, which also affect bee populations (Westrich 1996; Roulston & Goodell 2011). A broad array of nesting habitats, substrates, and building materials are used by different bee species (Potts *et al.* 2005), and the specific nest site requirements of bee species (e.g. presence of bare soil, dead wood or pithy stems) may limit their populations in contemporary intensified anthropogenic landscapes (Steffan-Dewenter & Schiele 2008; Chapter 6). In many simplified, intensively used agricultural landscapes, linear landscape features such as field boundaries are one of the few remaining semi-natural habitats that may provide nesting resources. These field boundaries are often dominated by dense grassy vegetation due to eutrophication (Kleijn & Verbeek 2000). Such field boundaries probably lack suitable nesting sites for most ground-nesting solitary bees, as these generally require bare soil or sparsely vegetated patches to build their nests (Potts *et al.* 2005; Sardiñas & Kremen 2014), and their suitability as nesting sites appears to be mainly restricted to a few common bumblebee species (Svensson *et al.* 2000; Kells & Goulson 2003). For bees nesting above-ground in dead wood or pithy stems field boundaries have even less nesting resources to offer. Nesting ecology and the availability of suitable nesting sites may therefore be as important as host plant preference and floral resource availability in determining bee species' susceptibility to decline under land use change. However, relatively little is known about the nesting requirements of most bee species. While we were able to determine host plant preference of bees and estimate changes in the availability of preferred host plants over the course of the 20th century, it is extremely difficult to quantify nest site requirements of bees in a similar fashion and determine trends in the availability of suitable nesting sites for different bee species.

Increased use of pesticides associated with agricultural intensification is also suspected as a serious threat to bees (Potts *et al.* 2010). Particularly the increasing application of systemic neonicotinoid insecticides since the early 1990s has caused concern (Van der Sluijs *et al.* 2013). Depending on the dose and duration of exposure, pesticides can have lethal (Alston *et al.* 2007) or sublethal effects on bees, with the latter negatively affecting foraging efficiency, colony growth, reproduction and susceptibility to disease and parasites (Vidau *et al.* 2011; Gill *et al.* 2012; Feltham *et al.* 2014; Sandrock *et al.* 2014). As such, exposure to pesticides may contribute to wild bee decline. The observed negative effects of loss of preferred floral resources in our study may for instance have been amplified by negative sub-lethal effects of exposure to pesticides on foraging behaviour and efficiency. However, like nesting preference and nest site availability, it is very difficult to quantify exposure and vulnerability of different bee species to pesticides and assess their impact on long-term national population trends. It may be expected that bees that preferably forage on flowering crops are most exposed to pesticides. Yet, in our study we found that bee species that mainly collect pollen from crop plant families have stable or increasing populations. This may indicate that, although pesticides may impact bee fitness, the use of pesticides has been of minor importance in driving long-term bee population trends in The Netherlands.

Although it remains unknown to what extent wild bee decline is caused by other factors, we convincingly linked the decline of wild bee species to the decline of their preferred pollen host plants (Chapter 2). These host plants provide the pollen sources essential for offspring production: provisioning brood cells with non-host pollen leads to lower offspring fitness or no offspring production at all (Praz *et al.* 2008; Sedivy *et al.* 2011). Furthermore, we showed that larger bee species were more susceptible to decline under land use change, probably because of their larger pollen quantity requirements (Müller *et al.* 2006). Together, population trends of pollen host plant and bee body size explained 46% of the variation in bee population trends. Therefore, until we have a better understanding of the importance of the other proposed factors, most importantly nest site availability, enhancing floral resources remains the most promising management option to mitigate bee decline in contemporary agricultural landscapes. Yet, our results highlight the importance of targeting the specific host plants of bee species, for many declining species most notably plant species of the Fabaceae and Lamiaceae families.

Effectiveness of mitigation measures

While current conservation actions to promote bees in agricultural landscapes generally aim to directly or indirectly enhance floral resources, these agri-environmental measures have produced variable results (e.g. Kleijn *et al.* 2006). We hypothesised that the effectiveness of agri-environmental measures is a function of (1) agricultural management intensity at the field scale (e.g. agro-chemical inputs, stocking rates) (Kleijn & Sutherland 2003), (2) the percentage of semi-natural habitat in the surrounding landscape (Tscharntke *et al.* 2005) and (3) the ecological contrast induced by the measures (Chapter 3). The introduced concept *ecological contrast* refers to the extent to which implemented agri-environmental measures improve habitat conditions compared to conventionally managed sites. Effects of agri-environmental measures are thus expected to increase with the size of the ecological contrast created by the measures, for instance in terms of improvement of floral resource availability.

Using a meta-analytic approach, we showed that the effectiveness of agri-environmental measures is mainly driven by the ecological contrast in floral resources produced by the measures (Chapter 4). Moreover, we provided the first conclusive evidence for the landscape complexity hypothesis, with measures being more effective at enhancing pollinators in structurally simple landscapes with intermediate proportions of semi-natural habitat, than in landscapes nearly devoid of semi-natural habitat or with large proportions of semi-natural habitats. Our transect field study on effectiveness of wildflower strips (Chapter 5) furthermore suggest that the combined effects of ecological contrast and landscape context are mainly driven by the interplay of local and landscape-wide floral resource availability. Provided that there are sufficient floral resources to support source populations in the wider landscape, a larger local increase in floral resources results in a larger local increase in bee richness and abundance, irrespective of the surrounding landscape. However, the same degree of enhancement of local floral resource availability results in larger effects on local bee abundance and richness in relatively flower-poor than in relatively flower-rich landscapes. These insights suggest that effectiveness of management interventions to promote bees can be enhanced by maximizing the effects of the interventions on floral resource availability.

While we found clear support for the effects of local and landscape floral resources on effectiveness of agri-environmental measures in enhancing bee species richness and abundance, the results of both the meta-analysis (Chapter 4) and the field study (Chapter 5) did not enable us to distinguish between population responses and spatio-temporal behavioural aggregation responses. In other words, we cannot conclude from these results whether enhancing floral resources enhanced bee reproduction and population growth, or just attracted bees from the surrounding landscape to the created resource-rich sites. This illustrates that population-level responses of mobile species such as bees are difficult to assess based on observations of species richness and abundance of foraging bees. In our trap nest study (Chapter 6) we show that directly measuring population dynamical variables, such as reproduction, can be used to assess population-level effects of wildflower strips. However, although wildflower strips appeared to enhance brood cell production of some cavity-nesting bee species, we did not find unequivocal evidence for actual population growth. These moderate effect sizes may suggest that the strips did not contain sufficient amounts of the preferred host plants and/or the two-year monitoring period after establishment was too short to detect clear population responses. Nevertheless, the discrepancy between the effectiveness of wildflower strips in enhancing forager densities (Chapter 5) and population growth (Chapter 6) stresses the importance of setting clear objectives and evaluation criteria for agri-environmental measures (Chapter 3). Measures that only affect foraging responses can be considered effective if the objective is to promote pollination in adjacent crops, but these measures do not help the plight of the bee species that are in decline.

Management implications

Our results suggest that bees are influenced by environmental factors operating at both the field and landscape scale (Chapters 4 and 5). We therefore stress the importance of employing a landscape-scale perspective in strategies for bee conservation. Agri-environmental measures to promote bees appear to be most effective in structurally simplified, resource poor landscapes. However, the relatively large positive effects of generic agri-environmental measures in the simple, resource poor landscapes are probably mainly restricted to common generalist species that are able to persist in these landscapes (Dormann *et al.* 2007). In contrast, species of conservation concern, which are mainly restricted to structurally complex, resource-rich landscapes that harbour the most species rich bee communities (Tscharntke *et al.* 2005; Franzen & Nilsson 2008; Le Féon *et al.* 2010), probably benefit little from generic agri-environmental measures (Kleijn *et al.* 2006). We therefore argue that conservation of intrinsic values of bee diversity requires a different approach than efforts that aim to promote pollination services in agricultural landscapes (Chapters 3 and 4).

Conservation of rare and endangered species

Bee species differ in their response to land use change and agricultural intensification (Larsen *et al.* 2005; Bommarco *et al.* 2010; Williams *et al.* 2010) and, consequently, some species decline sharply, whereas others remain stable or even thrive under current environmental change pressures (Biesmeijer *et al.* 2006; Bartomeus *et al.* 2013). We showed that this species-specific nature of wild bee decline is for a large part driven by pollen host plant preference: bee species that have declined and have become rare depend on plant species that have declined (Chapter 2). Loss of plant diversity in north western Europe is mainly driven by eutrophication, desiccation, and acidification associated with land use change (Runhaar *et al.* 1996; Roem & Berendse 2000; Kleijn *et al.* 2009). Declining bee species have therefore mainly become confined to the less affected semi-natural habitats and nature reserves that still contain their host plants (Franzen & Nilsson 2008; Kohler *et al.* 2008). Not surprisingly, a reduction in the amount of semi-natural habitat in landscapes results in increased similarity of bee communities (Dormann *et al.* 2007), indicating that as semi-natural habitat is lost local bee communities are increasingly being dominated by the same common, generalist species. Thus, although semi-natural areas may provide habitat for both common and rare bee species, they appear to be especially important for providing the resources that limited population size of the rare ones.

Conservation aimed at protecting and promoting rare and threatened bee species should therefore focus on extensively managed, structurally complex landscapes that support species rich bee communities (Pywell *et al.* 2012; Chapter 3). Here, semi-natural habitats should be protected to prevent further habitat loss and fragmentation. In addition, the management of existing habitats and/or the creation of new habitats such as wildflower strips should, to be effective (Pywell *et al.* 2012; Reemer *et al.* 2012; Chapter 5), specifically target the host plants of the bee species of conservation concern (Chapter 2). General agri-environmental measures on farmland are probably less effective in enhancing the host plants of these species, as these species are often difficult to establish on farmland, for example because of their specific requirements for growth conditions (Bakker & Berendse 1999; Pywell *et al.* 2003), low seed availability in the seed bank (Blomqvist *et al.* 2003) or limited seed dispersal (Ozinga *et al.* 2009).

As briefly discussed in the previous section, it is important to distinguish between spatio-temporal behavioural responses and population-level responses when evaluating the effectiveness of conservation actions that aim to promote threatened and rare bee species. In our field study on the effectiveness of wildflower strips, the large observed effects in terms of forager densities (Chapter 5) did not (yet) reflect clear population enhancement of bees (Chapter 6), suggesting that the large effects mainly reflect spatio-temporal aggregation responses. If the intrinsic values of biodiversity are the primary objective, initiatives resulting in behavioural responses without any additional population-level responses should be considered ineffective (Chapter 3). Monitoring population dynamics is therefore essential in evaluating the effectiveness of these initiatives.

Promoting pollination services

The majority of crop visitation, a proxy for pollination services (Vázquez *et al.* 2005), is performed by common, widespread species. A recent global analysis of 90 studies on crop-visiting bee communities shows that, although on average 23.6 wild bee species were observed visiting crop flowers in each study, the single most abundant species accounted for 39.5% of all visits, and only five bee species accounted for 80% of crop visitation (Kleijn & Scheper 2013). Threatened or rare species were largely absent and only accounted for 0.3% of the observed crop visits. For plants it has been shown that habitat loss and agricultural intensification mainly result in the loss of rare and subdominant species, whereas dominant species are largely unaffected (Kleijn *et al.* 2009). The same pattern has been suggested for bees (Dormann *et al.* 2007), and ongoing research indeed shows that the dominant crop-visiting species are not affected by loss of semi-natural habitat (Kleijn *et al.* in review). These dominant crop pollinating bee species have stable or increasing population trends (Bartomeus & Winfree 2013; Chapter 2) and are able to persist in structurally simple, intensively farmed landscapes. However, in such landscapes the absolute total abundance and richness of crop-visiting wild bees is relatively low (Le Féon *et al.* 2010; Ricketts *et al.* 2008) while demand for pollination may be relatively high and expected to increase (Breeze *et al.* 2014; Schulp *et al.* 2014). This makes potential yield gaps from pollination deficits most imminent in these landscapes (Deguines *et al.* 2014). Efforts to promote pollination service should therefore preferentially be directed at the structurally simple landscapes dominated by insect-pollinated crops.

Dominant crop pollinators are relatively easily enhanced by agri-environmental measures (Kleijn & Scheper 2013), which we have shown to be most effective in exactly the structurally simple landscapes (Chapter 4). The often relatively nitrophilous host plants of these bee species can be fairly easily promoted with general conservation measures on farmland (Pywell *et al.* 2003; Kleijn *et al.* 2006). Although a lot can be gained if management of existing uncultivated farmland habitats aims to indirectly facilitate the development of more flower-rich vegetation, such as adapting mowing regimes in field margins (Noordijk *et al.* 2009), directly enhancing floral resources by establishing wildflower strips is particularly effective (Chapters 4 and 5). Establishment of such flower rich habitats has been shown to increase flower visitation and crop yield in adjacent insect-pollinated crops (Morandin & Kremen 2013; Blaauw & Isaacs 2014). For the dominant crop-visiting bumblebee species, in Europe most notably *Bombus terrestris/lucorum* and *Bombus lapidarius* (Kleijn & Scheper 2013), it is essential to ensure a continuous supply of floral resources during their entire colony cycle (Rundlöf *et al.* 2014, Chapter 5).

While behavioural responses are a poor measure for evaluating the effectiveness of conservation efforts to promote threatened bee species, it is no problem to use such responses to evaluate the effectiveness of efforts to promote pollination services (Chapter 3). After all, for the pollination of crops it does not matter whether increased crop flower visitation results from behavioural foraging responses or enhanced populations. Yet, if the objective is to ensure sustainable, stable delivery of pollination services, especially under expected increase in pollination demand, effectiveness of pollination supporting practices should also be evaluated by the extent to which they lead to actual population enhancement of the most important pollinator species. Ultimately, these practices should be evaluated by their effect on crop yield and economic costs and benefits (Blaauw & Isaacs 2014).

The way forward

In this thesis we convincingly linked the decline of wild bee species to the loss of their preferred host plants. However, as outlined above, changes in the availability of suitable nesting sites may be equally important in driving national bee population trends. Furthermore, it remains unclear to what extent bee species are currently limited by nest site availability in agricultural landscapes and how this impacts on the delivery of pollination services. In Chapter 6 we found that most of the investigated above-ground, cavity-nesting bee species were probably limited by nest site availability in agricultural landscapes. For the conservation of wild bee biodiversity as well as the promotion of pollination services it is therefore essential to address both food and nesting resources. Yet, particularly little is known about the extent to which ground-nesting bees, which from the large majority of the bee species in Europe, are limited by nesting sites in contemporary agricultural landscapes and how this can be remedied. Consequently, the role of nest site availability currently remains one of the most significant knowledge gaps in our understanding of the factors driving bee population dynamics. Further research is required to identify the requirements for nesting site and nest building material of different bee species and to examine how selection of nest location is affected by other factors such as local availability of floral resources.

With respect to management to promote pollination services it is important to identify whether and under what conditions the yield of different crops is currently limited by pollination by wild pollinators, and how this relates to limitation by other inputs such as fertilizer or pest control (Lundin *et al.* 2013; Melathopoulos *et al.* 2014; Motzke *et al.* 2015). As argued above, yield gaps associated with pollination deficits are probably greatest in simplified intensive landscapes. To alleviate these yield gaps it is essential to understand their underlying mechanism. An important question in this context is whether optimal pollination, both in terms of crop yield and quality, can be achieved if only the few dominant crop-visiting species are available. Although the abundance of these species does not decline with decreasing proportion of semi-natural habitats, the abundance of other species does (Dormann *et al.* 2007; Kleijn *et al.* in review), and consequently total crop visitation rate decreases when semi-natural habitat is lost (Ricketts *et al.* 2008; Garibaldi *et al.* 2011). In parallel, seed set and crop yield decrease with decreasing proportion of semi-natural habitat (Garibaldi *et al.* 2011; Martins *et al.* 2015). However, whether this results from a reduction of total crop visitation rate, which could be remedied by simple measures to enhance the abundance of the dominant crop pollinators, or the specific contribution of the subdominant crop-visiting bee species, remains unclear. Quantitative measures of flower-visitation and pollen deposition may be poor proxies for pollination (King *et al.* 2013; Garibaldi 2013) and both experimental (Albrecht *et al.* 2012) and field studies (Hoehn *et al.* 2008; Rogers *et al.* 2014; Gagic *et al.* 2015; Martins *et al.* 2015) suggest that (functional trait) diversity of crop-pollinating bee communities may be more important than the absolute abundance of crop visits for pollination and yield. The question therefore rises to what extent functional diversity of wild bee communities in intensively farmed landscapes, composed of only a few dominant crop pollinators, is sufficient for optimal pollination. If optimal pollination requires larger functional diversity, what are the marginal gains in pollination and yield of habitat management practices that also aim to enhance abundances of the less common crop-visiting species? Does this outweigh the associated costs? Of course, also in the case where large abundances of just a few dominant species are required to provide sufficient pollination, adoption of management practices to enhance the abundance of these species depends on their cost-effectiveness. From an applied perspective, these remain the most important questions regarding the enhancement of pollination and yields of insect-pollinated crops.

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SUMMARY

Accumulating evidence suggests that many wild bee species have declined over the last decades in Europe. As the most important pollinator species, wild bees play an essential role in ecosystem functioning and the delivery of pollination services to crops. In addition to concern about loss of intrinsic values of bee biodiversity, reported wild bee declines have therefore raised concerns about both loss pollination services and increased the need for effective measures to mitigate bee loss. Land use change and agricultural intensification since the second half of the 20th century are considered the most important drivers of wild bee decline. It is generally believed that these environmental pressures drive bee decline through loss of floral resources, but so far this has been largely based on speculation. Nevertheless, current conservation actions to promote bees in agricultural landscapes generally focus on the direct or indirect enhancement of floral resources. Such agri-environmental measures have however produced variable results, with effectiveness varying greatly among different types of measures and across landscapes and regions. Identifying the main causes for bee decline and understanding the mechanisms that explain the variation in effectiveness of mitigation measures are essential to develop and implement effective measures to promote wild bees in agricultural landscapes. The aims of this thesis were therefore twofold: i) to investigate whether and to what extent wild bee decline is driven by loss of floral resources in contemporary intensively used agricultural landscapes, and ii) to investigate what environmental factors drive the effectiveness of measures that aim to promote bees, and specifically assess to what extent the effects of these environmental factors are mediated by effects of floral resource availability.

In **Chapter 2** we used a trait-based approach and historic population trend estimates of bee species and their pollen host plants to examine the role of loss of floral resources in driving wild bee decline in The Netherlands. We showed that bee body size and pollen host plant preference were the two main factors explaining population trends of different bee species between the periods 1902–1949 and 1975–1999. Population trends of bee species were positively related to the trends of their preferred host plants: as specific plant species declined, so too did the bee species that depended on them. Particularly the host plants of bee species that are active later in the season displayed strong declines. Interestingly, bee species that mainly depended on pollen from plant families that contain major insect-pollinated crops such as apple, strawberry, oil-seed rape, and sunflower, have stable or increasing populations. Bee body size was negatively related to population trend: especially the larger species, which have larger pollen quantity requirements, declined. Taken together, these results strongly suggest that loss of preferred floral resources has driven the population decline of many wild bee species in The Netherlands.

In **Chapter 3** we reviewed what is known about the mechanisms that affect the effectiveness of conservation measures on farmland, with effectiveness defined as the extent to which biodiversity is enhanced in sites under agri-environmental management compared to conventionally managed control sites. We discussed two existing hypotheses regarding effects of land use intensity and landscape complexity. First, according to the *land use-moderated conservation effectiveness hypothesis* effectiveness of agri-environmental measures declines nonlinearly with increasing land-use intensity at the field scale (e.g. rates of agrochemical inputs and agricultural disturbances). As a result, the largest impacts of agri-environmental measures are expected in relatively extensively managed sites, because in very intensively farmed areas a reduction in disturbance rates in sites under agri-environmental management is still insufficient to support many species. Second, the *landscape-moderated conservation effectiveness hypothesis* predicts that effects of agri-environmental measures should be more pronounced in structurally simple landscapes (1–20% semi-natural habitat) than in cleared (<

1% semi-natural habitat) or complex landscapes (> 20% semi-natural habitat). Effects are expected to be smaller in complex landscapes because these landscapes support large species pools and biodiversity is already high everywhere. In cleared landscapes with hardly any semi-natural habitat effects are also expected to be limited, but in this case because too few source populations remain to respond to implantation of agri-environmental measures. In contrast, in simple landscapes source populations are still present, allowing significant responses to implementation of measures. In addition to these two hypotheses, we introduced the concept *ecological contrast*, which refers to the extent to which implemented agri-environmental measures improve habitat conditions compared to conventionally managed sites. Effects of agri-environmental measures are expected to increase with the size of the ecological contrast created by the measures, for instance in terms of improvement of floral resource availability. We combined these three hypotheses in a framework that proposes that the effectiveness of agri-environmental measures is a function of agricultural management intensity at the field scale, the percentage of semi-natural habitat in the surrounding landscape, and the ecological contrast induced by the implemented measures.

Using a meta-analytical approach, this framework was tested in **Chapter 4**. This meta-analysis was based on 71 primary studies that addressed the effects of agri-environmental measures on pollinators in Europe, which besides wild bees included hoverflies and butterflies. We found that agri-environmental measures generally enhance species richness and abundance of pollinators, but, as hypothesised, the magnitude of the effects depended on landscape context and the ecological contrast induced by the measures. Contrary to expectations, land use intensity did not affect effectiveness. Measures were more effective at enhancing pollinators in structurally simple than in cleared or complex landscapes and effectiveness of measures increased with increasing induced ecological contrast in floral resource availability. Establishment of sown flower strips, which directly enhance floral resources and thereby readily create relatively large ecological contrasts, proved to be a particularly effective measure to enhance pollinator species richness and abundance. However, few of the investigated agri-environmental measures were specifically targeted at pollinators and the positive effects of the general agri-environmental measures were probably mainly restricted to common generalist species that are able to persist in structurally simplified, resource poor landscapes. Species of conservation concern, which are mainly restricted to structurally complex landscapes that harbour the most species rich bee communities, probably did not benefit from general agri-environmental measures.

In **Chapter 5** we performed an in-depth analysis of whether the variation in bee responses across landscape and regions to introduction of mitigation measures is primarily explained by the interplay of the local and landscape-wide floral resource availability. To this end, we performed a transect field study in four European countries. In each country we established wildflower strips using the same seed mixture of mid- to late-season flowering forage plants specifically targeted at bees. Furthermore, we employed a three-year before-after-control-impact (BACI) design to examine whether establishment of wildflower strips resulted in actual enhancement of bee populations or merely spatio-temporal behavioural aggregation responses. Our study showed that wildflower strips generally enhanced local bee abundance and richness compared to conventionally managed control field boundaries, including Red Listed species, but the effect depended on the interplay between the degree of enhancement of local flower richness in the strip and the amount of floral resources in the surrounding landscape. The patterns for the effects of landscape-wide floral resource availability differed however between species groups: effects on solitary bees decreased with increasing amount of floral resources in the surrounding landscape, whereas effects on bumblebees increased with increasing early-season landscape-wide floral resource availability, reflecting their dependence on seasonal continuity of food resources. Based on the observed foraging responses in our study we could not demonstrate population-level effects of the wildflower strips, suggesting that the positive effects mainly reflected spatio-temporal behavioural aggregation responses rather than enhanced bee population sizes.

The field study showed that on the basis of transect observations population-level effects of mitigation measures are hard to assess for mobile species such as bees. In **Chapter 6** we therefore used artificial trap nests to measure reproductive responses of cavity-nesting bee species to establishment of wildflower strips. Using the same three-year BACI design of the transect field study, we assessed whether and under what conditions wildflower strips enhance bee population growth. We found that effects of wildflower strips were species-specific: brood cell abundance of *Osmia* spp. was significantly enhanced, whereas patterns for *Heriades truncorum* and *Megachile* spp. were less clear, and no effects at all were observed for *Hylaeus* spp. Although wildflower strips enhanced reproduction of *Osmia* spp., this only became apparent in the second year after establishment. We therefore did not find unequivocal evidence for population effects of wildflower strips for any of the species. The moderate effect sizes may suggest that the size of the strips was too small and/or the two-year monitoring period after establishment was too short to detect clear population responses. Nevertheless, the differential responses across taxa suggest that population-level effects of wildflower strips may likely depend on the match between bees' host plant preference and the plant species composition of the strips. We furthermore found that most species displayed increasing brood cell production, in both wildflower strips and control field boundaries, after introduction of the artificial trap nests. This indicates that the host plants of the investigated cavity-nesting bee species are probably not limiting their populations, and rather suggests that the populations of these species are more limited by nest site availability in contemporary agricultural landscapes.

This thesis highlights the role of loss of preferred floral resources in explaining the species-specific nature of wild bee decline. It furthermore shows that the effectiveness of agri-environmental measures in promoting bees mainly depends on the extent to which the measures enhance floral resources and on the composition of the surrounding landscape. We therefore argue that efforts to promote wild bees require a landscape-scale perspective, with different approaches for biodiversity conservation, targeted at threatened and rare species, and pollination service objectives, targeted at the few common species dominating crop-visiting bee communities. Efforts to promote species of conservation concern require specific measures that aim to enhance the declining host plant species of endangered bee species. These measures should be implemented in structurally complex, heterogeneous landscapes that still contain source populations. In contrast, the common host plant species of dominant crop-pollinating bee species can be relatively easily enhanced with generic agri-environmental measures. These measures should be implemented in simple, homogeneous landscapes where yield gaps from pollination deficits are most likely to occur. While our findings provide important insights in the role of floral resources in driving bee populations, still little is known about the extent to which wild bee populations are currently limited by nesting sites, and how this affects bee population trends and the delivery of pollination services in agricultural landscapes. This is currently the most important knowledge gap in the development of management practices to promote wild bees.

SAMENVATTING

Veel wilde bijensoorten zijn de afgelopen decennia in Europa afgenomen. Bijen zijn de belangrijkste bestuivers van de meeste wilde planten en landbouwgewassen, en spelen als zodanig een essentiële rol in het functioneren van ecosystemen en de productie van insectbestoven landbouwgewassen. De achteruitgang van wilde bijen heeft dan ook, naast bezorgdheid over consequenties voor de intrinsieke waarde van bijenbiodiversiteit, geleid tot ongerustheid over verlies van de bestuivingsdiensten die wilde bijen leveren, en een dringende noodzaak voor maatregelen om wilde bijen te bevorderen. Veranderd landgebruik en de intensivering van de landbouw sinds de tweede helft van de 20^e eeuw worden beschouwd als de belangrijkste oorzaken voor de achteruitgang van wilde bijen. Het wordt over het algemeen aangenomen dat deze factoren de achteruitgang van wilde bijen veroorzaken via hun negatieve effecten op de beschikbaarheid van bloemen in de huidige agrarische landschappen, maar vooralsnog is dit grotendeels gebaseerd op speculatie. Desondanks richten huidige maatregelen om bijen in agrarische landschappen te bevorderen zich vooral op het, direct of indirect, vergroten van het bloemaanbod. Dergelijke agrarische natuurbeheersmaatregelen laten echter wisselende resultaten zien, waarbij de effectiviteit van maatregelen sterk kan verschillen tussen verschillende typen maatregelen, landschappen en regio's. Voor het ontwikkelen en implementeren van effectieve maatregelen is het essentieel om inzicht te verkrijgen in de belangrijkste oorzaken voor hun achteruitgang, en grip te krijgen op de ecologische mechanismen die de effectiviteit van bevorderende maatregelen voor wilde bijen bepalen. De doelstelling van dit proefschrift was daarom tweeledig: i) onderzoeken of en in hoeverre de achteruitgang van wilde bijen wordt veroorzaakt door het verlies van bloemen in de hedendaagse intensief gebruikte agrarische landschappen, en ii) inzicht verkrijgen in hoe verschillende omgevingsfactoren de effectiviteit van bevorderende maatregelen beïnvloeden, en specifiek in welke mate de effecten van deze omgevingsfactoren verlopen via effecten van bloembeschikbaarheid.

In **Hoofdstuk 2** hebben we, op basis van de soortspecifieke eigenschappen van verschillende bijensoorten en de historische populatietrends van de bijensoorten en hun geprefereerde waardplanten, de rol van het verlies van voorkeurswaardplanten als drijvende factor voor de achteruitgang van wilde bijen in Nederland onderzocht. We hebben laten zien dat lichaamsgrootte en waardplantvoorkeur de belangrijkste verklarende factoren zijn voor de populatietrends van de verschillende soorten bijen tussen de perioden 1902–1949 en 1975–1999. De populatietrend van bijen was positief gecorreleerd met de populatietrend van hun waardplanten: als bepaalde waardplanten achteruit gingen, gingen ook de bijensoorten achteruit die hier bij voorkeur op foerageerden. Vooral de waardplanten van bijensoorten die laat in het seizoen actief zijn, zijn sterk achteruit gegaan. Opvallend genoeg hebben bijensoorten die vooral afhankelijk zijn van stuifmeel van plantenfamilies waartoe belangrijke insectbestoven gewassen zoals appel, aardbei, koolzaad en zonnebloem behoren stabiele of toenemende populaties. De lichaamsgrootte van bijensoorten was negatief gecorreleerd met hun populatietrend: vooral grotere soorten, die grotere hoeveelheden stuifmeel nodig hebben, zijn achteruit gegaan. Tezamen bieden deze resultaten sterke aanwijzingen dat het verlies van geprefereerde bloemensoorten ten grondslag ligt aan de achteruitgang van veel wilde bijensoorten in Nederland.

In **Hoofdstuk 3** hebben we doormiddel van literatuuronderzoek verkend wat er bekend is over de mechanismen die de effectiviteit van natuurbehoud op boerenland beïnvloeden, waarbij effectiviteit gedefinieerd is als de mate waarin de biodiversiteit wordt bevorderd op percelen onder agrarisch natuurbeheer in vergelijking met gangbaar beheerde controlepercelen. We behandelden twee bestaande hypothesen over de effecten van landgebruiksintensiteit en landschapscomplexiteit op effectiviteit van agrarisch natuurbeheer.

Volgens de eerste hypothese, de *landgebruik-afhankelijke effectiviteit van agrarisch natuurbeheer hypothese*, daalt de effectiviteit van agrarische natuurbeheersmaatregelen niet-lineair met toenemende intensiteit van het landgebruik op perceelsschaal (de mate van verstoring door agrarische werkzaamheden zoals bijvoorbeeld maaien, beweiden, grondbewerking of het gebruik van agrochemische middelen). Als gevolg hiervan worden de grootste effecten van agrarisch natuurbeheer verwacht in relatief extensief beheerde gebieden, omdat op locaties met zeer intensieve landbouw een vermindering van de agrarische verstoringen door implementatie van agrarisch natuurbeheer nog steeds onvoldoende is om habitat voor veel soorten te kunnen bieden. De tweede hypothese, de *landschap-afhankelijke effectiviteit van agrarisch natuurbeheer hypothese*, voorspelt dat de effecten van agrarische natuurbeheersmaatregelen groter zijn in structureel *simpele* landschappen (1-20% semi-natuurlijke habitat) dan in *kale* (<1% semi-natuurlijke habitat) of *complexe* landschappen (> 20% semi-natuurlijke habitat). In complexe landschappen zijn de te verwachten effecten kleiner, omdat deze landschappen grote bronpopulaties kunnen bevatten en de biodiversiteit daardoor overal al relatief hoog is. In kale landschappen met nauwelijks semi-natuurlijk habitat zullen de effecten naar verwachting ook beperkt zijn, maar in dit geval omdat er te weinig bronpopulaties aanwezig zijn om te reageren op de implementatie van agrarische natuurbeheersmaatregelen. In simpele landschappen zijn daarentegen bronpopulaties nog steeds in voldoende mate aanwezig, waardoor relatief grote effecten van implementatie van maatregelen kunnen optreden. Naast deze twee bestaande hypothesen, introduceerden we het concept *ecologisch contrast*, dat verwijst naar de mate waarin de implementatie van agrarische natuurbeheersmaatregelen de omstandigheden voor soorten verbetert ten opzichte van gangbaar beheerde percelen. Effecten van agrarische natuurbeheersmaatregelen zullen naar verwachting toenemen met de grootte van het door de maatregelen gecreëerde ecologische contrast, bijvoorbeeld met betrekking tot verbetering van het bloemaanbod. We combineerden deze drie hypotheses in een theoretisch kader dat stelt dat de effectiviteit van agrarische natuurbeheersmaatregelen een functie is van agrarisch beheersintensiteit op perceelsschaal, het percentage semi-natuurlijk habitat in het omringende landschap en het door de geïmplementeerde maatregelen gecreëerde ecologische contrast.

Dit theoretisch kader hebben we in **Hoofdstuk 4** getest door middel van een meta-analyse. Deze meta-analyse is gebaseerd op 71 primaire studies die de effecten van agrarisch natuurbeheer op aantallen en soortenrijkdom van bestuivers, met naast bijen ook zweefvliegen en vlinders, hebben onderzocht. Agrarische natuurbeheersmaatregelen bevorderen over het algemeen de aantallen en soortenrijkdom van bestuivers, maar zoals verwacht hing de grootte van de effecten af van de landschapscontext en het ecologische contrast dat werd gecreëerd door de maatregelen. In tegenstelling tot onze verwachtingen had landgebruiksintensiteit geen invloed op de mate van effectiviteit van de maatregelen. Maatregelen waren meer effectief in het bevorderen van bestuivers in structureel simpele dan in kale of complexe landschappen en de effectiviteit van de maatregelen nam toe met de grootte van het door de maatregelen gecreëerde ecologische contrast in bloembeschikbaarheid. Het inzaaien van bloemenstroken, wat direct de beschikbaarheid van bloemen verbetert en daarmee relatief makkelijk een vrij groot ecologisch contrast creëert, bleek een bijzonder effectieve maatregel om de aantallen en soortenrijkdom van bestuivers te bevorderen. Echter, slechts enkele van de onderzochte agrarische natuurbeheersmaatregelen waren specifiek op het bevorderen van bestuivers gericht, en de positieve effecten van generieke maatregelen op bestuivers zijn waarschijnlijk voornamelijk beperkt tot algemene, generalistische soorten die in staat zijn zich te handhaven in de structureel simpele, relatief arme landschappen. Zeldzame en bedreigde soorten, die vrijwel alleen nog in structureel complexe, soortenrijke landschappen gevonden worden, profiteerden waarschijnlijk niet van deze generieke maatregelen.

In **Hoofdstuk 5** hebben we vervolgens meer specifiek gekeken of en in hoeverre de variatie in effecten van maatregelen die in verschillende landschappen en regio's zijn geïmplementeerd verklaard kunnen worden door de wisselwerking van lokale en landschap-brede beschikbaarheid van bloemen. Hiertoe hebben we een transectstudie uitgevoerd in vier Europese landen. In elke land hebben we bloemenstroken ingezaaid, waarbij in elk land het zelfde zaadmengsel gebruikt is, bestaande uit specifiek op bijen gerichte, midden tot laat in het seizoen bloeiende, waardplanten. Daarnaast gebruikten we een zogenaamde "before-after-control-impact" (BACI) onderzoeksopzet om te ontrafelen of het inzaaien van bloemenstroken leidt tot daadwerkelijk populatiegroei van wilde bijen, of slechts tot spatio-temporele veranderingen in gedrag (concentratie-effecten). Onze studie toonde aan dat bloemenstroken over het algemeen de lokale abundantie en soortenrijkdom van bijen bevorderen, inclusief Rode Lijstsoorten, maar de effectiviteit van de bloemenstroken was afhankelijk van de wisselwerking tussen de mate van verbetering van de lokale bloemrijkdom door de strook en de hoeveelheid bloemen in het omringende landschap. De invloed van de landschap-brede beschikbaarheid van bloemen verschilde echter tussen verschillende groepen bijen: effecten van bloemenstroken op solitaire bijen namen af met toenemende hoeveelheid gelijktijdig met de bloemenstroken bloeiende bloemen in het omringende landschap, terwijl de effecten op hommels toenamen met toenemende beschikbaarheid van vroeg in het seizoen bloeiende bloemen in het landschap. Dit laatste weerspiegelt de afhankelijkheid van hommels van een continue bloemaanbod gedurende het hele seizoen. Op basis van onze waarnemingen van foeragerende bijen konden we geen effecten van bloemenstroken op populatieniveau aantonen, wat suggereert dat de waargenomen positieve effecten van de stroken voornamelijk het gevolg waren van aggregaties van foeragerende bijen in de bloemstroken, in plaats van toegenomen bijenpopulaties.

De transectstudie in Hoofdstuk 5 laat zien dat het, voor mobiele soorten zoals bijen, moeilijk is om op basis van waarnemingen in transecten te beoordelen of bevorderende maatregelen tot populatie-effecten leiden. In **Hoofdstuk 6** hebben we daarom gebruik gemaakt van kunstmatige nestgelegenheden (zogenaamde "bijenhotels") om de effecten van bloemenstroken op de reproductie van holte-nestelende bijensoorten te onderzoeken. Op basis van dezelfde BACI opzet als in de transectstudie hebben we onderzocht of en onder welke omstandigheden het inzaaien van bloemenstroken leidt tot populatiegroei van bijen. We vonden dat de effecten van de bloemenstroken soortspecifiek waren: de aanleg van bloemenstroken leidde tot significant hogere aantallen broedcellen van metselbijen (*Osmia* spp.), terwijl de patronen voor de tronkenbij (*Heriades truncorum*) en bladsnijderbijen (*Megachile* spp.) minder duidelijk waren, en er geen enkel effect op maskerbijen (*Hylaeus* spp.) werd waargenomen. Hoewel de reproductie van metselbijen door de bloemenstroken werd bevorderd, kwam dit effect pas in het tweede jaar na aanleg duidelijk naar voren. We hebben daarom voor geen van de onderzochte soorten ondubbelzinnig bewijs gevonden voor populatie-effecten van bloemenstroken. Mogelijk was de grootte van de bloemenstroken te klein en/of de tweejarige monitoringsperiode na aanleg van de stroken te kort om duidelijke populatie-effecten te kunnen waarnemen. Desalniettemin suggereren de verschillende patronen voor de verschillende soortengroepen dat de mate van populatie-effecten van bloemenstroken waarschijnlijk afhangt van de overeenstemming tussen de waardplantvoorkeur van bijensoorten en de plantensamenstelling in de stroken. We zagen verder dat de reproductie van de meeste bijensoorten toenam, in zowel de bloemenstroken als de controle akkerranden, na plaatsing van de bijenhotels. Dit wijst er op dat de beschikbaarheid van waardplanten de populatiegroei van de meeste onderzochte bijensoorten waarschijnlijk minder sterk beperkte dan de beschikbaarheid van voldoende nestgelegenheid in hedendaagse agrarische landschappen.

Dit proefschrift laat zien dat de verminderde beschikbaarheid van voorkeurswaardplanten een belangrijke rol speelt in het verklaren van het soortspecifieke karakter van de achteruitgang van wilde bijen. Het toont verder aan dat de effectiviteit van de agrarische natuurbeheersmaatregelen in het bevorderen van bijen vooral afhangt van de mate waarin de maatregelen het bloemaanbod verbeteren, en van de compositie van het omringende landschap. Beleid om wilde bijen te bevorderen vereist dan ook een landschapsperspectief, met een verschillende aanpak voor maatregelen ten behoeve van het behoud van biodiversiteit, gericht op zeldzame en bedreigde soorten, en maatregelen ten behoeve van het bevorderen van bestuivingsdiensten, gericht op de enkele algemene soorten die de hoofdmoot van alle bestuivingsdiensten leveren. Behoud van zeldzame en bedreigde soorten vereist maatregelen die de achteruitgaande voorkeurswaardplanten van deze soorten bevorderen. Deze maatregelen zouden moeten worden uitgevoerd in structureel complexe, heterogene landschappen die nog bronpopulaties van de zeldzame bijensoorten bevatten. De algemene waardplanten van de dominante gewas-bestuivende bijensoorten kunnen daarentegen vrij eenvoudig worden bevorderd met generieke agrarische natuurbeheersmaatregelen. Deze maatregelen zouden met name geïmplementeerd moeten worden in structureel simpele, homogene landschappen waar problemen met suboptimale gewasopbrengsten als gevolg van onvoldoende bestuiving het meest te verwachten zijn. Hoewel onze bevindingen belangrijke inzichten bieden in de rol van bloembeschikbaarheid als drijvende factor voor populatieontwikkeling van wilde bijen, is er nog steeds weinig bekend over in welke mate bijenpopulaties tegenwoordig beperkt worden door voldoende aanbod van nestgelegenheid, en wat de consequenties hiervan zijn voor de populatietrends van verschillende soorten bijen en de levering van bestuivingsdiensten in agrarische landschappen. Dit vormt momenteel de belangrijkste kenniskloof in de ontwikkeling van beheersmaatregelen om wilde bijen te bevorderen.

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CURRICULUM VITAE

Jeroen Alexander Scheper werd geboren op 2 november 1978 in Hengelo, Overijssel. In 1997 behaalde hij zijn VWO diploma aan het Thijcollege in Oldenzaal. Aansluitend begon hij met de studie Bedrijfskunde aan de Rijksuniversiteit Groningen, waarvoor hij, jaren later, in januari 2005 zijn doctoraaldiploma behaalde. Na afsluiting van de studie Bedrijfskunde besloot hij om zijn passie voor ecologie en natuur te volgen en begon hij met de Masterstudie Bos- en Natuurbeheer aan de Wageningen Universiteit. Tijdens zijn studie heeft hij bij de leerstoelgroep Natuurbeheer en Plantenecologie twee afstudeeronderzoeken gedaan naar de ontwikkeling van vegetatiemozaïeken in begraasde bosweide systemen. In 2009 sloot hij zijn studie *cum laude* af. Hierna ging hij als onderzoeker werken bij de Stichting Graslandwetenschappen, waar hij onderzoek deed aan beweidingssystemen en tropische grassoorten. In 2010 verlegde hij zijn aandacht van “grote grazers” naar “kleine bestuivers” toen hij, onder begeleiding van prof. dr. ir. David Kleijn, als onderzoeker in opleiding bij Alterra begon met zijn promotieonderzoek naar bevorderende maatregelen voor wilde bestuivende insecten. Dit onderzoek heeft hij van 2010 tot en met 2014 uitgevoerd binnen het kader van het door de Europese Commissie ondersteunde project *Status and Trends of European Pollinators (STEP)* en het onderzoeksprogramma *BIJ-1* van het Ministerie van Economische Zaken. De resultaten van dit onderzoek zijn, onder begeleiding van co-promotor prof. dr. ir. David Kleijn en promotoren prof. dr. Henk Siepel en prof. dr. Joop Schaminée, beschreven in dit proefschrift. In februari 2015 kreeg Jeroen als “postdoc” onderzoeker een aanstelling bij de leerstoelgroep Resource Ecology van prof. dr. Herbert Prins, waar hij zich opnieuw toelegde op onderzoek naar wilde bestuivers. Na de benoeming van David Kleijn als hoogleraar van de leerstoelgroep Plantenecologie en Natuurbeheer verhuisde hij op 1 juli 2015 mee naar deze groep, en keerde daarmee terug naar de voorheen geheten leerstoelgroep Natuurbeheer en Plantenecologie.

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