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Scaling up effects of measures mitigating pollinator loss from local- to landscape-level population responses

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Abstract

1. Declining pollinator populations have caused concern about consequences for food production, and have initiated an increasing number of initiatives that aim to mitigate pollinator loss through enhancement of floral resources. Studies evaluating effects of mitigation measures generally demonstrate positive responses of pollinators to floral resource enhancement. However, it remains unclear whether this represents landscape-level population effects or results from a spatial redistribution of individuals from otherwise unaffected populations.

2. Here, we present a method for estimating landscape-level population effects using data from commonly used standardized pollinator transect surveys. The approach links local density responses of pollinators in both mitigation sites and surrounding landscape elements to the area these habitats occupy in mitigation landscapes as well as control landscapes to obtain landscape-level population estimates.

3. We demonstrate the method using data from a 2-year study examining the effects of experimental wildflower enhancements on wild bumblebees and solitary bees in Dutch agricultural landscapes. The results show that conclusions based on local responses may differ significantly from those based on landscape-level responses.

4. Wildflower enhancements significantly enhanced landscape-level abundance of both bumblebees and solitary bees. Bumblebees showed a pronounced positive local density response in mitigation sites and the surrounding landscape that was in line with significant landscape-level increases in abundance. However, solitary bees showed no local response to mitigation sites, and the landscape-level increases in abundance only became apparent when the area of bee habitat was taken into account.

5. Incorporating the area of both newly created and pre-existing pollinator habitats into effect estimates accounts for density-dependent processes such as dilution, spillover and local concentration of individuals. It, therefore, results in more reliable

estimates of the response to mitigation measures of pollinators, as well as other mobile arthropod groups that are often being surveyed using transect surveys.

1 | INTRODUCTION

The expansion and intensification of agriculture is resulting in the rapid replacement of natural and semi-natural habitats by crop monocultures and consequently in the decline of biodiversity across the globe (Donald, Green, & Heath, 2001; Kremen, Williams, & Thorp, 2002). Especially in developed countries, conservation measures such as wildflower strips (Blaauw & Isaacs, 2014; Tschumi, Albrecht, Entling, & Jacot, 2015), wild bird seed mixtures (Baker, Freeman, Grice, & Siriwardena, 2012) or restrictions in the use of agrochemicals (Pywell et al., 2012) are being implemented on farmland to counteract the loss of wild species from agricultural landscapes. Initially the focus of these measures was primarily on conserving biodiversity for the sake of biodiversity itself (Kleijn et al., 2006). More recently, the objective increasingly became the safeguarding of the ecosystem services biodiversity provides to farmers and human society in general, such as pest control, pollination and recreation. Pollination, in particular, has appealed to the imagination of scientists, policymakers and the general public, probably because 76% of the leading global food crops are dependent upon animal pollination (Klein et al., 2007). Concern about consequences of declining pollinator populations (Biesmeijer et al., 2006) has inspired a wealth of pollinator conservation initiatives. Apart from traditional conservation initiatives such as government-funded agri-environment schemes, an increasing number of smaller scaled pollinator conservation actions are being taken by, for example, multinationals, city councils, farmers or concerned citizens.

Despite a vast body of literature examining the responses of pollinators to conservation management (Dicks, Showler, & Sutherland, 2010), to date, effects of local measures on population levels at the landscape scale are largely unknown. Unlike studies on birds, which often examine landscape-level effects of local mitigation measures (e.g. Baker et al., 2012; Gillings, Newson, Noble, & Vickery, 2005), pollinator studies are rarely carried out at the landscape scale. Most studies compare pollinator densities at control sites and at sites with management that aims to mitigate pollinator loss (i.e. mitigation sites). Such studies generally find pollinators to be significantly more species-rich and abundant in mitigation sites than in control sites although this response can be moderated by habitat quality and context of the surrounding landscape (Haaland, Naisbit, & Bersier, 2011; Scheper et al., 2013). Whether these higher densities are the result of overall larger populations or caused by behavioural responses resulting in a redistribution of otherwise unaffected populations is unclear. Although the exact area requirements of vital pollinator

populations are not well understood (Dicks et al., 2015; Kremen, Williams, Bugg, Fay, & Thorp, 2004) mitigation sites by themselves are probably rarely large enough to sustain viable populations of target species and the species to be enhanced are expected to deliver their services in the arable fields, orchards and vineyards in the landscape surrounding the mitigation sites.

Determining landscape-level effects on pollinators of local measures is complicated because most pollinator species are highly mobile. Unlike birds, nest sites of most pollinators are difficult to locate and therefore cannot be reliably quantified (but see Carvell et al., 2017; Wood, Holland, Hughes, & Goulson, 2015). This means that scientists have to infer population effects from the responses of foraging individuals. Depending on species group, individuals may drift through the landscape using resources as they encounter them (e.g. hoverflies; Jauker, Diekotter, Schwarzbach, & Wolters, 2009) or may selectively and repeatedly utilize resource-rich patches within the foraging range around a nest (bees; Osborne et al., 1999). In any case, measures enhancing resource availability in one place will affect the spatial distribution of the population in the rest of the landscape (Hanley et al., 2011; Holzschuh, Dormann, Tscharntke, & Steffan-Dewenter, 2011). This makes comparisons of local population densities in sites with and without measures, the most commonly used approach to evaluate the impact of measures, difficult to interpret because it does not give insight into the net effect at the landscape level (Kleijn, Rundlof, Scheper, Smith, & Tscharntke, 2011).

Recent studies have begun using a more informative approach of examining population responses of pollinators in the wider landscape surrounding mitigation sites (e.g. Blaauw & Isaacs, 2014; Carvell, Bourke, Osborne, & Heard, 2015; Feltham, Park, Minderman, & Goulson, 2015; Jonsson et al., 2015; Morandin & Kremen, 2013). However, these approaches only measure local density responses such as the number of individuals per transect. Landscape-level population size is determined by the product of pollinator density in a habitat and the area in the landscape occupied by that habitat. Studies that do not consider the size of the newly created pollinator habitats can produce ambiguous results. This is illustrated in Figure 1 where panels a–c depict a number of possible density responses in mitigation sites and in pollinator habitats in the surrounding landscape. In scenario a, local pollinator densities in both mitigation sites and the wider landscape are not significantly different from those in control landscapes. This response is generally considered to indicate failure of conservation measures to enhance pollinators (Jonsson et al., 2015). If the mitigation site is small such a response is indeed unlikely to result in a significantly higher number of pollinators at
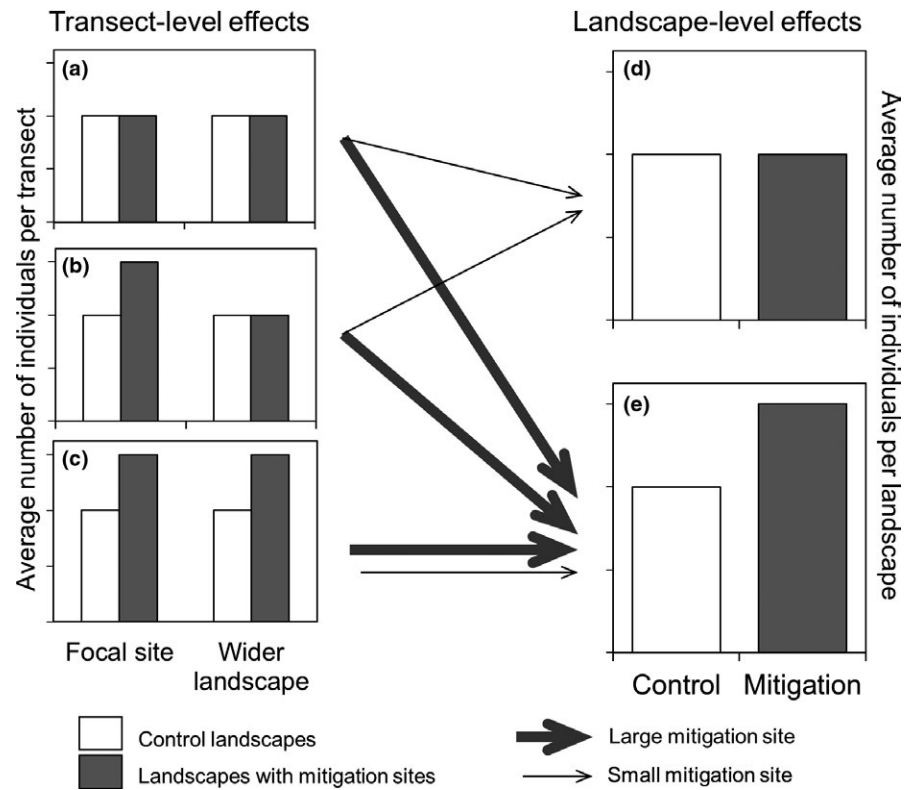
FIGURE 1 An illustration of a number of plausible effects of the establishment of wildflowers on farmland on local (transect-level) pollinator density in mitigation sites and in the surrounding landscape and how this may translate into landscape-level abundance effects

the landscape level (panel d). However, if the mitigation site is large and replaces habitat that is of no value to pollinators, as is generally the case in Europe where mitigation is often implemented on intensively managed crop fields (Pywell et al., 2015; Tschumi et al., 2015; Wood, Holland, & Goulson, 2015; Wood, Holland, Hughes, et al., 2015), this would mean that the cover of pollinator habitat in the landscape increases significantly. If all this new habitat is supporting densities similar to those in pre-existing habitats, this could result in significantly more pollinators at the landscape level (panel e). Panel b depicts a scenario where local population densities are enhanced in mitigation sites while local densities are unaffected in the surrounding landscape. Such a response is usually presented as evidence for measures delivering biodiversity benefits (panel e; for example, Carvell, Meek, Pywell, Goulson, & Nowakowski, 2007; Jonsson et al., 2015; Tschumi et al., 2015). However, if mitigation sites are very small, the mitigation-induced increase in number of individuals may be negligible compared to the landscape-level population size in which case this local enhancement effect will not result in landscape-level population increases (panel d). Panel c depicts a response in which local population densities are enhanced in both the mitigation sites and the surrounding landscape. This is the only scenario of density responses that unequivocally indicates landscape-level increases in pollinator numbers. Of course, the spatial scale at which landscape-level responses can be expected will differ between species (groups) and are probably related to their foraging range.

Whether or not local density responses are indicative of landscape-level population effects may, therefore, depend on both the effect size of the density response and the size of the new

mitigation site relative to pre-existing pollinator habitat and whether these are related. So far, the importance of size of the newly created mitigation sites has mainly been demonstrated through their moderating effects on local population densities (Carvell et al., 2011; Heard et al., 2007; Jonsson et al., 2015; Scheper et al., 2015). The implications of these relations for landscape-level population effects are unclear (Scheper et al., 2015). Here, we demonstrate how landscape-level responses to measures mitigating pollinator loss can be scaled up from local density responses in mitigation sites and pre-existing habitats in the surrounding landscape using wild bees as a model system. We use results from a 2-year study in 20 study areas in Dutch agricultural landscapes. In half of the study areas, we established wildflower mixtures; the other half were used as paired controls. In the first and second year of flowering we surveyed local bee densities using standardized transect surveys in mitigation sites and in linear landscape elements (e.g. field boundaries, roadside verges, railway embankments) at increasing distances from the mitigation sites. In control landscapes we surveyed bees in linear landscape elements only using the same spatial sampling design. In each study area we quantified the cover of pre-existing linear landscape elements. We calculated landscape-level bee numbers by multiplying local bee densities with the area of the mitigation site and/or the area of linear landscape elements at a range of spatial scales. We used these data to ask (1) Is pollinator density in mitigation sites related to the size of the mitigation area, (2) Do transect-level data indicate positive local- or landscape-level effects of mitigation sites on bees, and (3) are the results from the landscape-level data in line with those from the transect-level data? We asked these questions separately for bumblebees and solitary bees as they have different

foraging ranges and are known to respond differently to conservation management (e.g. Scheper et al., 2015).

2 | MATERIALS AND METHODS

2.1 | Study sites

In 2012, we selected 20 study areas in agricultural landscapes located across the central and southern parts of the Netherlands (See Figure S1 in Supporting Information). We selected landscapes mostly dominated by grasslands, maize and winter wheat and without mass-flowering crops as these are known to (temporarily) strongly influence pollinator densities (Hanley et al., 2011; Holzschuh et al., 2016) and may therefore complicate our interpretations of pollinator responses to mitigation practices. On arable fields at the centre of 10 study areas we sowed wildflower seed mixtures designed to mitigate pollinator loss. In each area, two different wildflower mixtures were used in equal proportions with one targeting long-tongued bee species, the other short-tonged bees, hover flies and parasitoid wasps (Table S1). Differences in bee species composition between mixtures were outside the scope of this paper and the pooled area sown with the two mixtures was therefore considered as the wildflower field or the mitigation site. Eight sites were sown in fall 2012, the remaining two followed in spring 2013. In fall 2013, vegetation was cut and removed to suppress the dominance of spontaneously established grasses and optimize flower availability in 2014. The mean size of the area sown with wildflowers was 2.4 ha but ranged between study areas from 0.4 to 4.9 ha. The shape of the wildflower patches differed between areas with some being established as field margin strips along the crop edge and others as a consecutive block on (part of) a field. Each of the remaining 10 study areas served as a control and was paired with a mitigation area that had similar soil type and landscape context but did not have wildflower fields (Table S2). The minimum distance between the two study areas within a pair was 2.3 km (mean and maximum distance 6.5 and 15.3 km respectively), which is well beyond the average foraging range of the largest bee species occurring in our landscapes (Redhead et al., 2016).

2.2 | Landscape composition

In the Netherlands, agricultural fields are intensively managed, contain few or no flowers and we, therefore, assumed these habitats did not host any pollinators. In Dutch agricultural landscapes, wild pollinator populations are supported by two types of semi-natural habitats. Semi-natural grasslands and heathlands that are maintained for biodiversity conservation in protected areas represent the primary habitat for bee populations. From these habitats, populations of bees spillover into the linear landscape features of the surrounding agricultural matrix (Kohler, Verhulst, van Klink, & Kleijn, 2008). Linear landscape elements such as ditch banks, roadside verges, forest edges, railway banks and hedgerows represent secondary habitats for most wild pollinator species since they are generally eutrophicated, species-poor and contain relatively few flowering

plant species (Kleijn & Verbeek, 2000) and nest sites. We assumed that landscape-level effects of mitigation sites could be observed in linear landscape elements but not in protected areas that act as population sources themselves. In each of the 20 study landscapes we, therefore, separately quantified the proportional cover of heathlands and grasslands inside protected areas (hereafter semi-natural habitats) and linear landscape elements using ArcGIS version 10.0 (ESRI, Redlands, CA). In mitigation areas we did this in 500 m buffers around the wildflower fields. In control landscapes we first superimposed on the centre of the study area the shape of the wildflower field of the paired mitigation landscapes and then calculated cover of semi-natural habitats and linear landscape elements in a 500 m buffer to make sure we obtained comparable estimates from the two areas within each pair. The cover of semi-natural habitats was somewhat higher in landscapes with measures mitigating pollinator loss (M = 25.2 ha, range: 3.9–64.7 ha) than in control landscapes (M = 16.5, range: 7.5–25.0 ha). This difference was mainly due to two pairs (Table S2) and was not statistically significant (ANOVA, $F_{1,9}$ = 3.53, p = .093). Nevertheless we included semi-natural habitat cover in all our analyses to account for the variation in this variable. The cover of linear landscape elements did not differ systematically between study areas with and without mitigation (9.4 ha vs. 9.3 ha respectively; ANOVA, $F_{1,9}$ = 0.01, p = .91). The size of the wildflower patches was not correlated with the cover of semi-natural habitats or linear landscape elements (correlation coefficients, respectively, 0.10, t_8 = 0.785 and −0.31, t_8 = 0.384). To be able to extrapolate transect-level results to landscape-level results at different spatial scales we also calculated cover of linear landscape elements in buffers of 50 m (average total size of the area of the mitigation area and the buffer: 10.0 ha), 150 m (26.6 ha), 250 m (48.1 ha), 350 m (76.7 ha) and 450 m (122.6 ha) around each mitigation site. In control areas we did this around the superimposed shape of the mitigation site in the paired mitigation area.

2.3 | Bee sampling

In each study area, bees were sampled once a year by means of transect surveys (Westphal et al., 2008). Sampling was done between 09.00 and 17.30 hr on dry, warm (>15°C) and sunny days from early July to mid-August in 2013 and 2014. In study areas with mitigation sites we randomly located five 1 × 20 m transects in these wildflower fields. In the surrounding landscape we randomly selected 10 transects in linear landscape elements, such as roadside verges and ditch banks. Five transect plots were located at 50 m (±20 m) and five transect plots at 150 m (±50 m) from mitigation sites. Control landscapes were sampled using a similar spatial design and on the same day as the paired mitigation area. First, we located five transect plots in linear landscape elements at the centre of the study area. Subsequently, we sampled transect plots in linear landscape elements at 50-m (±20 m) and 150-m (±50 m) distance from the transect plots at the centre of the study landscapes. In each transect plot, all bees observed during a 10-min period (net observation time), regardless of whether they were visiting flowers, were

identified to species. Easily recognizable species were generally identified in the field; all other species were collected and identified in the laboratory. In the Netherlands, *Bombus terrestris* and *B. lucorum* workers and queens are extremely difficult to separate without molecular techniques, and so were grouped together. Honeybees *Apis mellifera* were observed but not included in the current analyses as abundance and distribution may be more strongly influenced by placement of hives than by our treatment.

Flower abundance was sampled concurrently with the bee sampling using an approach similar to that used by (Scheper et al., 2015). In each bee transect plot we counted the number of flowers or flower heads per plant of all species that are considered to provide resources for bees according to (Kirk & Howes, 2012). We measured the diameter of up to five flowers of any flowering plant species we encountered and used that to complement an existing plant species database with the average diameter of flowers for the observed species (Scheper et al., 2015). We obtained an estimate of the total area (m^2) of flowers per transect by summing the products of the average flower diameter and the number of flowers per species.

2.4 | Statistical analyses

2.4.1 | Transect-level responses

To analyse responses to enhancement of floral resources by bees at the transect level, we used linear mixed models on Ln-transformed bee abundance data. Inspection of residual plots confirmed that assumptions of normal and constant error distributions were satisfactorily met.

In an initial analysis we examined whether wildflower field size had an influence on local bee densities in and beyond the mitigation sites and whether this was influenced by the cover of semi-natural habitat. For this analysis we only used the 10 mitigation landscapes, because control landscapes did not contain sites with experimentally sown wildflower seed mixtures. In these analyses we included "study area" as a random factor to account for multiple observations within each study site. Fixed factors were 'wildflower field size," "distance" (classes 0 m, 50 m, 150 m), "year" (2013, 2014), "semi-natural habitat cover" and all two- and three-way interactions that included "wildflower field size." To correct for inherent qualitative differences between study areas, we included "within-transect flower abundance" as a covariate.

To analyse whether introducing wildflowers had an influence on local bee densities in and beyond the mitigation sites we initially conducted an integral analysis of the data from 2 years. We included "pair" and nested within pair, "study area" as random factors to account for multiple observations within each study site. Fixed factors were "mitigation" (wildflower field presence or absence), "distance," "year," "semi-natural habitat cover" and all possible interactions with mitigation in it. Within-transect flower abundance was again included as a covariate. For bumblebee abundance (but not for solitary bees) the three-way interaction mitigation × distance × year was significant ($F_{4,565.1}$ = 5.77, p < .001; Table S3) indicating that

bumblebee responses to wildflower field establishment differed between the 2 years at the three distance classes. Furthermore, semi-natural habitat cover did not influence the effects of mitigation for both species groups (all interactions p > .287; Table S3). We, therefore, subsequently chose to analyse the 2 years separately and used models including "within-transect flower abundance," "semi-natural habitat cover," "mitigation," "distance" and the interaction between mitigation and distance as fixed factors and "pair" and nested within pair, "study area" as random factors. In these analyses a significant mitigation × distance interaction would indicate that the effect of introducing wildflowers differs between distance classes (e.g. raising densities at 0 m but not at 50 m or 150 m). A significant mitigation effect without a significant mitigation × distance interaction would be indicative of landscape-level effects of introducing wildflowers.

2.4.2 | Landscape-level responses

To analyse responses to enhancement of floral resources of bee abundance at the landscape level we estimated the total number of bees (again separately for bumblebees and solitary bees) in mitigation and control landscapes in six increasingly large buffers around each mitigation site (0, 50, 150, 250, 350, 450 m). In landscapes with mitigation sites we did this by multiplying the average density of bees in the five transects (in individuals per m^2) in the wildflower plots with the total area of the wildflower plots (m^2). Since there were no statistically significant differences between bee densities observed at 50- and 150-m distance from mitigations sites (Table S4), we subsequently multiplied the average density in the 10 transects in the linear landscape elements in the surrounding countryside (individuals per m^2) with the total cover of these linear landscape elements (m^2) in the buffers around the wildflower plots. The sum of these two estimates represented our estimate of landscape-level bee abundance at a particular spatial scale (i.e. buffer size). In the control areas we multiplied the average density of bees in the 15 transects in linear landscape elements with the total cover of these landscape elements in the different buffers to obtain our estimate of landscape-level bee abundance. The natural logarithm of the total number of bumblebees and solitary bees per study area was subsequently related to mitigation (presence/absence) using linear mixed models assuming a normal error distribution. Cover of semi-natural habitats was included as a covariate to account for differences in semi-natural habitats between study landscapes. Pair was included as a random factor. All models were fitted using standard facilities in GenStat (Payne et al., 2002).

3 | RESULTS

The bee communities in our study areas were dominated by the bumblebees *Bombus lapidarius*, *B. terrestris/lucorum* and *B. pascuorum* and the solitary bees *Dasypoda hirtipes* and *Colletes daviesanus* (descending order of frequency of observations for both study years). In 2013, we observed 502 bumblebees of eight different

species and 270 solitary bees of 36 different species. Most likely due to poorer weather conditions the overall number of bees in 2014 was lower than in 2013, with a total of 247 individuals of eight bumblebee species and 207 individuals of 28 solitary bee species being observed. The mitigation sites had significantly higher wildflower cover than the pre-existing linear landscape elements (Appendix S1), with vegetation development resulting in larger differences in the second compared to the first year (respectively 5.6 vs. 3.2 times higher flower cover in mitigation sites than in the linear landscape elements serving as controls).

There was no significant overall relationship between wildflower field size and transect-level bumblebee densities and this relationship was furthermore not influenced by year or distance class (no significant interactions; Table S5). Semi-natural habitat cover did, however, affect the relationship between wildflower field size and bumblebee density (interaction $F_{1,5.8} = 7.03$, $p = .039$; Table S4). At low semi-natural habitat cover, bumblebee densities were relatively constant, while at high semi-natural habitat cover there was a 75% decline in bumblebee densities across the range of examined mitigation sizes (Figure 2). The size of the newly created wildflower fields was not in any way related to transect-level solitary bee density (Table S5).

In the first year after establishment of the wildflower fields, transect-level bumblebee densities showed a typical local enhancement effect (i.e. Figure 1b). In the mitigation sites themselves (0 m distance class) bumblebee densities were much higher than in control landscapes but in the landscape beyond the wildflower fields bumblebee densities were similar to those in control landscapes (Figure 3a, significant mitigation × distance class interaction, Table 1). In 2013, bumblebee densities were furthermore positively related to flower cover in the transects (Table 1). In the second year after establishment of wildflower fields, bumblebee densities tended towards a landscape-level enhancement effect (i.e. nearly significant mitigation effect in the absence of a mitigation × distance interaction; Figure 1c) with higher densities in mitigation landscapes both in the mitigation sites themselves and in the surrounding landscape (Figure 3c). In this year the interaction between mitigation and distance class was non-significant but the main effect of mitigation was almost statistically significant ($p = .056$; Table 1). In both years, distance class was significantly related to bumblebee density, which was largely caused by the pronounced increase in abundance in the mitigation sites, making the average for this distance class over both landscape types considerably higher than that of the other two distance classes. In both the first and second year after wildflower field establishment, transect-level solitary bee density did not show a response to mitigation in either the mitigation sites or the surrounding landscape (Figure 3b,d). The only observed significant relationship was with flower cover in the transect in 2013 (Table 1).At the landscape level, the extrapolated numbers of bumblebees were significantly higher in landscapes with mitigation sites than in control landscapes in both the first and the second year after wildflower field establishment (Figure 4a,c; Table S6). Differences
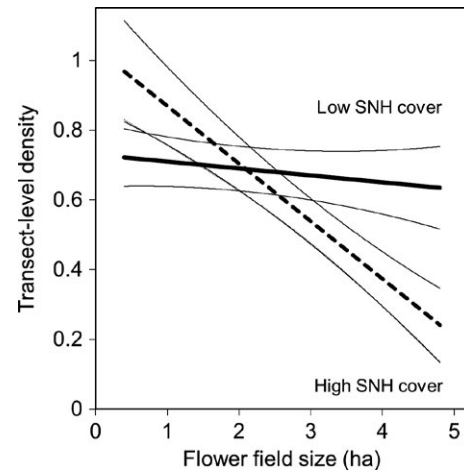

FIGURE 2 The influence of semi-natural habitat cover on the relationship between the size of wildflower fields and bumblebee density (ln(abundance + 1)) per transect in 2013 and 2014. High and low cover represent an average of respectively 8% (10 ha) and 33% (40 ha) semi-natural habitat (SNH) in a 500 m buffer around mitigation sites. Thin lines indicate standard errors

in landscape-level bumblebee numbers between mitigation and control landscapes became steadily smaller when spatial scales were considered that extended further beyond the mitigation sites. However, differences remained statistically significant up to the furthest considered scale of 450 m. Extrapolated solitary bee numbers were significantly larger in mitigation landscapes than in control landscapes at spatial scales of up to 150 m beyond mitigation sites in 2013, but only up to 50 m in 2014 (Figure 4b,d; Table S6).

4 | DISCUSSION

Evaluating the impact of measures mitigating the loss of arthropods at relevant spatio-temporal scales is of key importance for the design of effective strategies to enhance the provision of ecosystem services such as pollination in agricultural landscapes. The approach outlined in this paper expands upon existing standardized transect-based methodologies to assess landscape-level pollinator responses to habitat establishment. Incorporating the area of both newly created and pre-existing pollinator habitats into effect estimates allows us to take into account density-dependent processes such as dilution, spillover and local concentration of individuals. Such an approach, therefore, allows for a more straight-forward interpretation of the results and more robust conclusions.

Standardized transect surveys are the best available approach for examining interactions between pollinators and their environment (Westphal et al., 2008). However, local densities in single habitats are notoriously difficult to interpret because pollinator responses in one habitat are not independent from the patterns in other nearby habitats. The same patch of flowers may attract more pollinators in landscapes with few floral resources than in landscapes with many
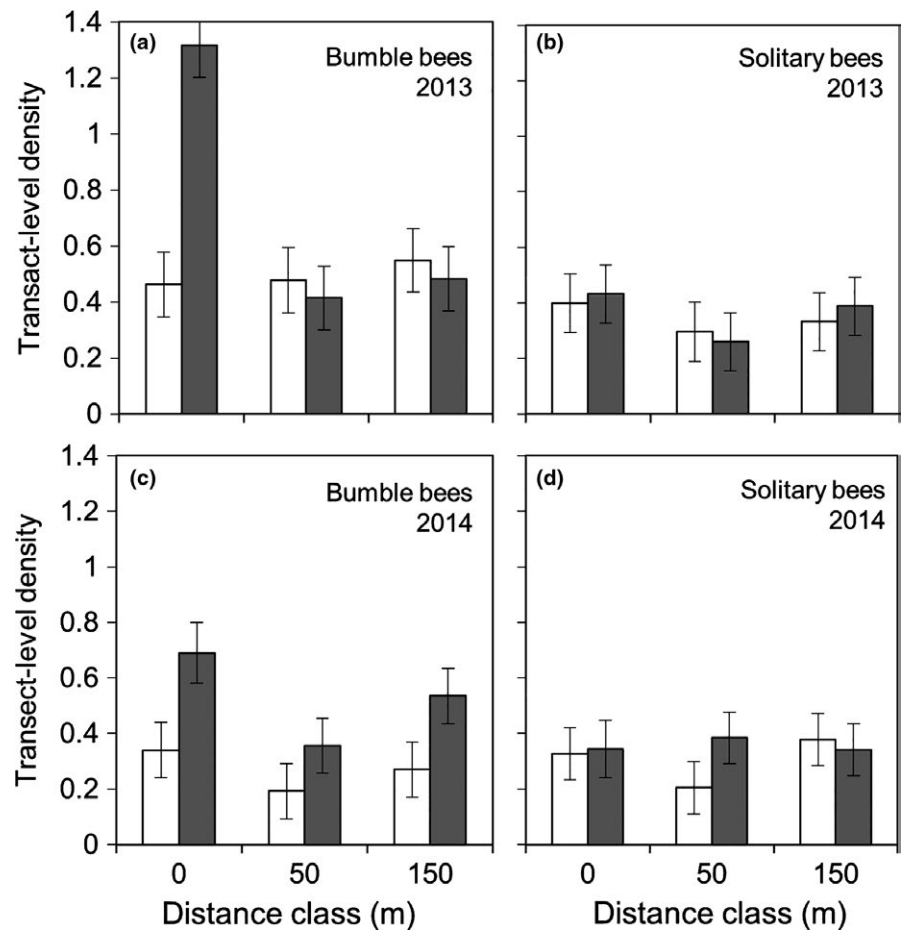
FIGURE 3 Transect-level responses of bumblebees and solitary bees (mean ln(abundance + 1) ±*SE*; *n* = 50) to experimentally established wildflower fields in and at two distances from the wildflower fields in the first (2013) and second year (2014) after establishment. Shaded bars indicate study landscapes with wildflower fields, open bars control landscapes

TABLE 1 Test results of Linear Mixed Models examining the relationship at transect level between Ln(bee abundance + 1) and the presence of a mitigation site, distance from the mitigation site and their interaction. The analyses corrected for differences in flower cover in the transect and cover of semi-natural habitat in the landscape. Landscape pair and, nested within pair, landscape identity were included as random factors

	Flower cover in transect		Semi-natural habitat cover		Mitigation		Distance class		Mitigation × Distance class	
	Test statistic	p	Test statistic	p	Test statistic	p	Test statistic	p	Test statistic	p
Bumblebees										
2013	$F_{1,287.5}$ = **9.62**	**.002**	$F_{1,16.1}$ = 0.5	.49	$F_{1,9.5}$ = 4.58	.06	$F_{2,282.6}$ = **25.74**	**<.001**	$F_{2,282.4}$ = **31.29**	**<.001**
2014	$F_{1,289.9}$ = 0.03	.856	$F_{1,14.6}$ = 0.32	.579	$F_{1,10.2}$ = 4.65	.056	$F_{2,276.2}$ = **7.74**	**.022**	$F_{2,276.3}$ = 1.38	.503
Solitary bees										
2013	$F_{1,297.2}$ = **24.43**	**<.001**	$F_{1,14.5}$ = 0.15	.702	$F_{1,9.6}$ = 0.02	.884	$F_{2,282.2}$ = 2.87	.239	$F_{2,282}$ = 0.34	.844
2014	$F_{1,290.5}$ = 0.74	.391	$F_{1,16.2}$ = 0.02	.899	$F_{1,10.2}$ = 0.31	.587	$F_{2,276.3}$ = 0.78	.677	$F_{2,276.4}$ = 2.33	.313

Test statistics in bold indicate significant effects at *p* < .05.

floral resources (Kleijn & van Langevelde, 2006). Many studies have highlighted the effects the amount of habitat in the landscape can have on observed pollinator densities (e.g. Holzschuh, Steffan-Dewenter, Kleijn, & Tscharntke, 2007; Hanley et al., 2011; Carvell et al., 2015; Jonsson et al., 2015; Holzschuh et al., 2016) but there is debate about the conclusions on landscape-level population sizes that can be drawn from these studies (Kleijn et al., 2011). As far as we know, no study has yet fully integrated the effects of habitat

quantity, both of the mitigation site and the pre-existing habitats in the wider landscape, to determine landscape-level pollinator responses. Our results show that by doing so, the conclusions with respect to the effects of mitigation may be different from those based on local density responses in and around mitigation sites alone and that they are probably more realistic.

Solitary bees showed a response depicted in Figure 1a with local densities in mitigation sites that were similar to those in
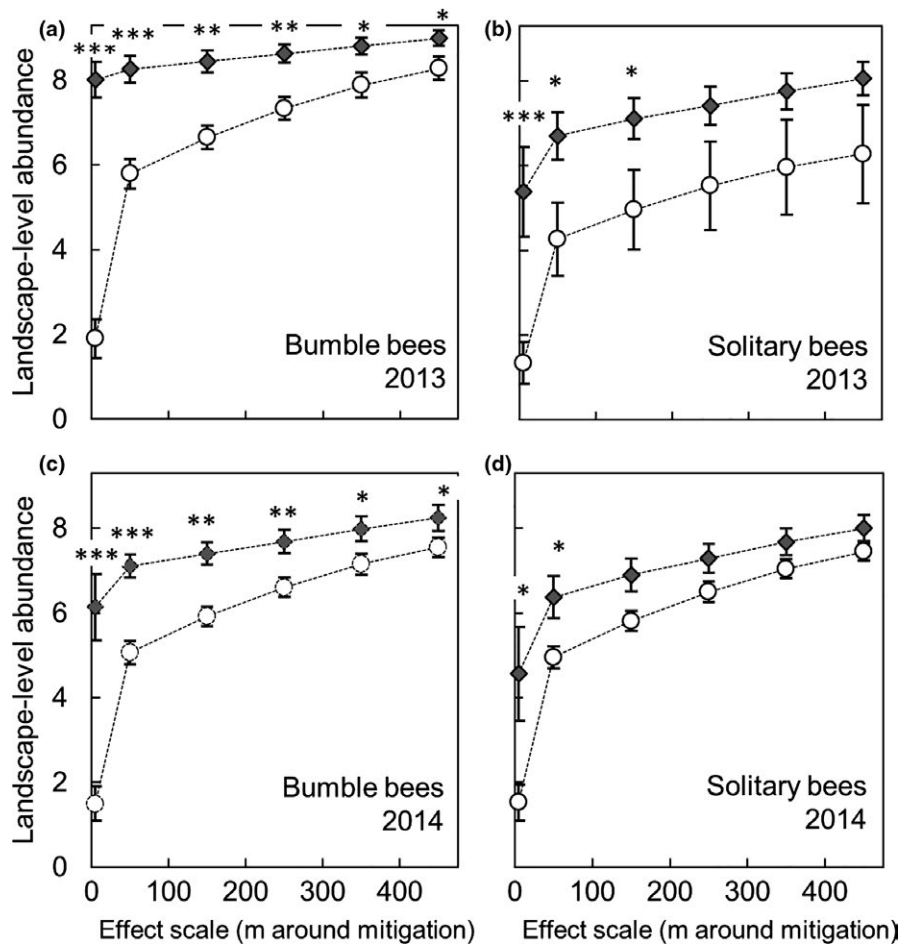
FIGURE 4 Extrapolated landscape-level responses of bumblebees and solitary bees (mean ln(abundance + 1) ±*SE*; *n* = 10) to experimentally established wildflower fields in the first (2013) and second year (2014) after establishment. Shaded bars indicate study landscapes with wildflower fields, open bars indicate control landscapes. Note that results of statistical tests at different effect scales are not independent of one another. *$p < .05$, **$p < .01$, ***$p < .001$

pre-existing linear landscape elements in control landscapes. Most solitary bees produce only one generation per year and mitigation-induced enhanced reproductive output could at best have contributed to population densities in the second year of the study. It is, therefore, surprising that making available vast amounts of floral resources to the resident bee population, from 1 year to the next, did not dilute the resident solitary bee population (no negative relationship between bee density and size of the mitigation sites in the first year; Table S5). Local bee densities often decrease with increasing landscape-level cover of mass-flowering crops (Holzschuh et al., 2011; Riedinger, Mitesser, Hovestadt, Steffan-Dewenter, & Holzschuh, 2015; Veddeler, Klein, & Tscharntke, 2006). The absence of such dilution effects in our study could have been caused by a number of different processes. First, larger mitigation sites could have attracted bees from larger distances. However, even though they may be physically capable of foraging at large distances from their nests (Zurbuchen, Cheesman, et al., 2010; Zurbuchen, Landert, et al., 2010) the high costs of long-distance foraging makes this an unlikely mechanism to independently explain the observed response. Natal dispersal, on the other hand, occurs over much larger distances than foraging trips. This is illustrated by the 200 km per year spread of the invasive *B. terrestris* in South America (Schmid-Hempel et al., 2014) even though in its native range it rarely forages beyond 2 km from the nest (Redhead et al., 2016). Furthermore,

greater access to nectar and pollen and reduced foraging times increase the life spans of flower visiting insects (Biesmeijer & Toth, 1998; Cahenzli & Erhardt, 2012; Smeets & Duchateau, 2003) which may have allowed foraging bees to visit larger wildflower patches for a longer period during the season. In combination, these processes may have resulted in the population size of solitary bees in the mitigation sites to grow proportionally with mitigation size. Studies into the behavioural and population dynamical responses of solitary bees to resource manipulations are needed to confirm this and would greatly help us understand and accurately predict population responses to measures mitigating pollinator loss.

In contrast to the analyses carried out at the transect level, landscape-level analyses showed enhanced solitary bee abundance in response to mitigation. The examined mitigation measures resulted in significantly higher solitary bee numbers in an area that included and extended beyond the mitigation sites for up to 50 m (2014) or 150 m (2013). In other words, introducing an average of 2.4 ha of wildflower fields significantly enhanced solitary bee numbers in an area of 10–26 ha. The positive larger-scale effects can be explained by the fact that the mitigation sites in our study mostly replaced crop monocultures that were inhospitable to bees. Introducing new habitats that support similar solitary bee densities as pre-existing habitats without a measurable reduction of bee densities in surrounding landscape elements add up to higher

landscape-level bee populations. Whether these positive landscape-level effects persist over time is unknown and will largely depend on how much floral resources the mitigation sites continue to provide. Long-term effects are generally unknown as most studies measure only in 1 or 2 years, with an occasional study lasting up to 4 years (Potts et al., 2009). The unexpectedly less pronounced response in the second compared to the first year probably had to do with the poorer weather conditions in 2014 compared to 2013. The average daily period with rain in July and August, our field work period, was more than three times longer in 2014 than in 2013 (1.9 vs. 0.6 hr/day; KNMI, 2015) which may have reduced bee foraging rate (Peat & Goulson, 2005; Tuell & Isaacs, 2010) so that available foraging time possibly limited pollinator population growth more than availability of floral resources.

Bumblebees produce multiple cohorts of workers within a season before they produce sexual offspring. Enhanced floral resources, therefore, not only improve the life span of individual bees but also allow bumblebees to produce workers faster and in larger numbers (Westphal, Steffan-Dewenter, & Tscharntke, 2006). This probably explains why bumblebees responded much more rapidly to the wildflower fields than the solitary bees. Figure 2 suggests that in areas with low cover of semi-natural habitats, and therefore probably few alternative floral resources, local bumblebee population size grew proportionally with the size of the wildflower fields resulting in overall constant local densities. In landscapes with high cover of semi-natural habitats, local densities declined with increasing size of the wildflower fields suggesting that here floral resources were probably no longer limiting bumblebee population growth. In line with previous studies (e.g. Heard et al., 2007), transect-level analyses demonstrated a strong local enhancement effect in the first year after establishment (compare Figure 3a with Figure 1b) which translated into a significant positive effect in the landscape-level analysis (Figure 4a). Possibly due to enhanced queen production in 2013, in 2014 bumblebees seemed to spillover into the wider landscape (Figure 3c; Figure 1c) which is indicative of the landscape-level population responses and in line with the results of the landscape-level analyses (Figure 4c). The landscape-level analyses furthermore suggest that positive landscape-level effects on bumblebees were observed at larger spatial scales than for the less mobile solitary bees and were still significant at the largest buffer size of 450 m around mitigation sites. Wildflower fields on average 2.4 ha in size significantly enhanced bumblebee numbers in up to 123 ha large landscape sectors. Bumblebees are known to temporarily spillover from flower-rich habitats such as mass-flowering crops onto nearby linear landscape elements without permanent population effects being apparent (Hanley et al., 2011). While behavioural responses could have contributed to the observed local density responses of bumblebees, the contrasting responses between 2013 and 2014 provide support for the conclusion that population dynamical processes are at the basis of this response. Mere behavioural responses should have resulted in the same patterns in both years. The contrasting responses of solitary bees and bumblebees highlight the importance of considering life-history traits such as generation time and foraging range

when designing or evaluating strategies to mitigate the decline of pollinators in agricultural landscapes.

Our calculation of the landscape-level population size assumes that local bee densities in high-quality protected areas are unaffected by the establishment of wildflower mixtures. In theory, the increase in bee densities in the mitigation sites could have been accompanied by reduced bee densities in these semi-natural habitats, thus, neutralizing landscape-level population effects. Since we did not observe a decline in transect-level bee densities in the linear landscape elements, we consider this an unlikely scenario. Nevertheless, measuring bee density responses in the high-quality semi-natural habitats as well as the lower quality linear landscape elements would further improve the reliability of the estimates of landscape-level pollinator responses of bees. Likewise, measuring local density responses over larger distances from mitigation sites will improve the reliability of the landscape-level population size estimates of more mobile species groups such as bumblebees. Our current estimates extrapolate the local density effects measured at a maximum of 150 m from mitigation sites to distances of up to 450 m. For bumblebees, but not for solitary bees whose local densities were not enhanced by the mitigation sites, this may have resulted in an overestimation of the landscape-level population size at the higher spatial scales. It is important to note that our approach assumes that the sampled linear landscape elements in the wider landscape are representative of linear landscape elements in general. Finally, because our approach uses a linear extrapolation of bee densities to habitat area, it is unsuitable for determination of landscape-level species richness responses. A straight-forward approach to do that has recently been described by (Wood, Holland, & Goulson, 2015) and uses species richness rarefaction curves based on all samples taken in an area.

The last decade has seen a continuing debate about whether conservation management is more effective when implemented in structurally simple, intensively farmed landscapes than in structurally complex, extensively farmed landscapes (Carvell et al., 2011; Holzschuh et al., 2007; Kleijn et al., 2011; Korpela, Hyvonen, Lindgren, & Kuussaari, 2013; Sole-Senan et al., 2014; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). This debate is largely based on studies that only take into account responses in mitigation and control sites without considering how conservation management affects biodiversity in the wider landscape (but see Carvell et al., 2015; Hammers, Muskens, van Kats, Teunissen, & Kleijn, 2015). The approach described in this paper accounts for the extent and relative importance of responses in both mitigation sites and the surrounding landscape. It, therefore, produces more robust conclusions about the effectiveness of management mitigating pollinator loss and generates more reliable recommendations for the optimal design and implementation of pollinator conservation strategies. The approach can easily be extrapolated to other mobile species groups, such as hover flies, butterflies, lady birds or lacewings that, like bees, are traditionally being surveyed using transect surveys. With increasing calls for more sustainable farming that is less dependent on external inputs and more reliant on ecosystem

services (Tscharntke et al., 2012), a reliable interpretation of the effects of our efforts to enhance key service providing organisms is pivotal.

AUTHORS' CONTRIBUTIONS

D.K., J.C.B. and F.L.W. designed the study. T.B., A.S. and T.E.W.L. collected the data. D.K. analysed the data and wrote a first draft manuscript and all authors provided suggestions to improve the manuscript.

DATA ACCESSIBILITY

Raw bee abundance data: Dryad Digital Repository https://doi.org/10.5061/dryad.51cd11j (Kleijn et al., 2018).

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