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Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe

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Agricultural intensification is one of the main causes for the current biodiversity crisis. While reversing habitat loss on agricultural land is challenging, increasing the farmland configurational heterogeneity (higher field border density) and farmland compositional heterogeneity (higher crop diversity) has been proposed to counteract some habitat loss. Here, we tested whether increased farmland configurational and compositional heterogeneity promote wild pollinators and plant reproduction in 229 landscapes located in four major western European agricultural regions. High-field border density consistently increased wild bee abundance and seed set of radish (*Raphanus sativus*), probably through enhanced connectivity. In particular, we demonstrate the importance of crop–crop borders for pollinator movement as an additional experiment showed higher transfer of a pollen analogue along crop–crop borders than across fields or along semi-natural crop borders. By contrast, high crop diversity reduced bee abundance, probably due to an increase of crop types with particularly intensive management. This highlights the importance of crop identity when higher crop diversity is promoted. Our results show that small-scale agricultural systems can boost pollinators and plant reproduction. Agri-environmental policies should therefore aim to halt and reverse the current trend of increasing field sizes and to reduce the amount of crop types with particularly intensive management.

1. Introduction

Pollinators provide essential services for the sexual reproduction of wild plant species, and they increase yield of many globally traded food crops and biofuels such as oilseed rape, coffee and cherry [1–3]. Therefore, reported wild pollinator declines are alarming, and could imperil future ecosystem stability and food security [4–6]. Key drivers of these pollinator declines are habitat loss and agricultural intensification [7]. Over the last century, European farmed landscapes have undergone socio-economic changes resulting in reduced cover of semi-natural vegetation, larger field sizes, simplified crop rotations and loss of crop diversity, with emphasis on a restricted number of cash crops [8,9].

Because semi-natural vegetation harbours diverse pollinator communities and supports pollination services [10,11], many agri-environment schemes attempt to compensate for biodiversity declines in agricultural landscapes by increasing the amount of semi-natural patches in these landscapes (e.g. by habitat restoration or by supporting high-nature-value farming). However, the global demand for agricultural products is predicted to increase during the coming decades due to human population growth and changes in consumption patterns [12]. Although improvements in food chain sustainability could mitigate these effects [13], it will be increasingly challenging to implement schemes that rely on taking land out of production or reducing farming intensity [14].

It has been suggested that increased heterogeneity of the crop fields at the landscape scale ('farmland') may promote biodiversity in agricultural landscapes without taking land out of production [15]. According to Fahrig *et al.* [15], farmland heterogeneity can be divided in two components. Farmland configurational heterogeneity describes the spatial arrangement of fields, and can be measured for example as mean field size or density of field borders. Farmland compositional heterogeneity describes the diversity of crops grown in a landscape, and can be measured as the Shannon diversity index of crop types.

Recent studies have aimed to disentangle the effects of landscape compositional and configurational heterogeneity on pollinators as understanding the relative importance of both components is essential [16], but mainly focused on the role of semi-natural vegetation patches. The few available studies investigating the impact of increased landscape configurational heterogeneity (e.g. number of patches per landscape, patch shape or interpatch connectivity) show contrasting results. Hopfenmüller *et al.* [17] found a positive effect on wild bee species richness, but other studies found no or only weak evidence that configurational heterogeneity influences pollinator communities [11,18,19], concluding that it is of minor importance for these highly mobile organisms. On the other hand, field borders in European agricultural landscapes are often accompanied by strips of varying sizes with semi-natural vegetation that can be herbaceous, woody or with bare ground [20]. These linear elements are important nesting sites [21] and also crucial for pollinator orientation [22,23]. Hence, high-field border density may guide pollinator movements, enhance habitat connectivity and thus increase the reproductive success of native pollinator-dependent plants [24]. Yet field borders with semi-natural boundaries might be more efficient in guiding pollinator movement due to better resource availability than simple crop–crop borders. To our knowledge it has not been tested whether smaller field sizes

resulting in more field borders can promote pollinators and plant reproduction.

Landscape compositional heterogeneity effects on pollinators and associated pollination services have been measured in a variety of ways. Most studies simply used the percentage of non-crop or semi-natural cover in the landscape as their measure of landscape composition [17,25]. Others measured the diversity of different cover types including crops and semi-natural habitats [11,19]. Most of these studies found that pollinators benefit from increasing landscape compositional heterogeneity. However, the effects of crop diversity on pollinators have been largely neglected by focusing only on certain crop types such as mass-flowering crops that provide ample resources for pollinators [26]. Crop diversity is expected to increase pollinator abundance, species richness and pollination services through complementary resource provisioning [15]. Different crop types are associated with different weed communities [27], and therefore provide different food resources, which pollinators in landscapes with high crop diversity can exploit [28,29]. However, crop identity might also play an important role and the relationship between pollinator diversity and compositional heterogeneity could also be unimodal [30], if the cover of certain crop types that are important for specialized species decreases with crop diversity. Nevertheless, we do not expect this, because pollinator species that are present in agricultural fields are usually generalists that can exploit a wide range of resources [31]. To our knowledge only Fahrig *et al.* [32] aimed at disentangling the effects of crop diversity and farmland configurational heterogeneity on pollinator diversity, but they did not investigate the link to ecosystem services.

Here we test whether farmland heterogeneity increases pollination services through increased pollinator abundance and species richness using a unique western Europe landscape-scale dataset. We sampled bees and hoverflies, and determined seed set of experimental phytometer plants, *Raphanus sativus*, in 229 fields within 94 landscapes distributed over four countries. Landscapes were selected to create independent gradients of farmland configurational and compositional heterogeneity. We also assessed the role of field borders in enhancing landscape connectivity for pollinators using a pollen transfer experiment testing whether transmission of fluorescent dye (a proxy for pollen) was enhanced along field borders. In particular, we addressed the following hypotheses: (1) landscapes with high configurational heterogeneity show higher pollination services, mediated by an increase in pollinator abundance and species richness due to enhanced connectivity and facilitated pollinator movement; and (2) landscapes with high compositional heterogeneity enhance pollination services mediated by increased pollinator abundance and species richness due to complementary resources provided by different crops.

2. Material and methods

(a) Landscape and site selection

The study was conducted in four European agricultural regions: France, Germany, Spain and the UK (electronic supplementary material S1 and S2, figure S1). Overall, we selected 94 agricultural landscapes, each with area 1 km² (32 in Germany, 30 in France, 20 in Spain and 12 in the UK, see electronic supporting material S2, 1.1 for details on the landscape selection process). For each selected landscape, we mapped the crop types of all fields during

Table 1 Description and measure of all explanatory variables used in the SEMs and in the pollen transfer experiment at the local and landscape scale.

		variable	description/measure	mean	min	max
pollinator survey and pollination experiment	landscape scale	configurational heterogeneity	field border density, measured as the length of all agricultural field borders (sum of field perimeters) per total crop area in the landscape (m ha^{-1}), includes crop–crop borders and semi-natural crop borders (see pollen transfer experiment)	285	68	625
		compositional heterogeneity	crop diversity, measured as Shannon diversity index using crop type richness and cover	0.96	0	1.6
		semi-natural cover	sum of area of all patchy non-forest habitats (e.g. semi-natural grasslands) and the area of linear semi-natural crop borders including grassy, woody and bare ground borders (%)	5.1	1.5	10.0
pollen transfer experiment	field scale	local flower cover	flower cover in a 3 m radius around the pan traps (%)	4.3	0	40
		crop field	arable crop field			
		crop–crop border	border between directly adjacent crops			
		semi-natural crop border	field border with semi-natural vegetation next to crop border			
		crop border type	type of adjacent crops (i.e. oilseed rape next to cereal or spring crop next to cereal)			

the cropping season and also their semi-natural border vegetation that varied across regions and included grassy, woody and bare ground borders. These data were digitized with ArcGIS software (ESRI, USA), and afterwards we calculated three landscape variables (table 1 for details and measures): (1) crop diversity (compositional heterogeneity; see electronic supplementary material S2, table S1 for a list of crop types included); (2) field border density (configurational heterogeneity); and (3) non-forest semi-natural cover. Forests were excluded, because intensively managed forests usually do not provide important food resources for pollinators [33]. This variable was dominated by the area of linear semi-natural vegetation which accounted for 68% of this variable across all four regions (electronic supplementary material S2, 1.2). We kept the proportion of non-forest semi-natural cover as low as possible as our main emphasis was on effects of crop compositional and configurational heterogeneity. The proportion of cultivated land was therefore high in all landscapes (mean \pm s.e.: $85 \pm 0.39\%$). We selected the landscapes such that gradients of compositional and configurational heterogeneity were uncorrelated, both overall and in each country (electronic supplementary material S2, figure S2).

In each landscape we chose three conventionally managed fields for sampling. We standardized sampled crop types within regions, because crop type might affect pollinator communities and we were not interested in local habitat effects, but in landscape-scale heterogeneity effects. To achieve gradients not biased by crop type in all regions some fields were excluded (electronic supplementary material S2, 1.3). This procedure resulted in 229 focal fields (1–3 fields per landscape; 69 in France, 94 in Germany, 45 in Spain and 21 in the UK). Focal fields within the 94 1 km^2 landscapes were at least 200 m apart from each other and at least 100 m from the landscape borders.

(b) Data collection

(i) Pollinator survey and pollination experiment

In each field we established two 50 m transects, one in the field edge and one in the field interior, where we installed pan traps for pollinator sampling (electronic supplementary material S2,

1.4 and figure S4). We conducted two surveys in 2013 (sampling dates in electronic supplementary material S2, table S2) and traps were operational for four consecutive days in each survey. Additionally, we estimated the percentage of flower cover of insect pollinated plant species in a radius of 3 m around each of the three poles per transect. Insects were stored in 70% ethanol, and all hoverflies were identified to species. Bees were classified as honeybee or wild bee for both transects in all countries. In addition, all wild bees were identified to species or morphospecies in Germany and Spain. In France only bee species from interior transects were identified, but as bee species richness of border and interior transects were highly correlated in Germany and Spain (Pearson's $r = 0.68$, $p < 0.001$) we assume that using only bee species richness from the interior transect in France did not bias the results. In the UK bees could only be classified as domestic (honeybees) or wild due to logistical and financial constraints.

To test the effects of farmland configurational and compositional heterogeneity on pollination services, we conducted a pollination experiment with common radish (*Raphanus sativus oleiferus*, Brassicaceae, REFORM variety, KWS, Germany), which is often used to assess insect pollination efficiency due to its dependence on insect pollination for reproduction [25,34]. Pollinators of radish include wild bees, honeybees, hoverflies and butterflies [34]. We placed two pots of radish at the edge transect of each field (electronic supplementary material S2, figure S4) for four days during the pollinator surveys in 2013 (sampling dates in electronic supplementary material S2, table S2). In Germany we conducted two sampling surveys (one during and one after oilseed rape bloom) and in France, Spain and the UK one pollination sampling survey (after oilseed rape bloom). To avoid seed loss, pods of the flowers that were open during field exposure (for details see electronic supplementary material S2, 1.5) were harvested shortly before full ripening. We counted the number of pods harvested from all plants of each field and the number of seeds enclosed in these pods.

(ii) Pollen transfer experiment

We examined the transfer of a pollen analogue (fluorescent dye) among experimental arrays of potted cornflowers (*Centaurea*

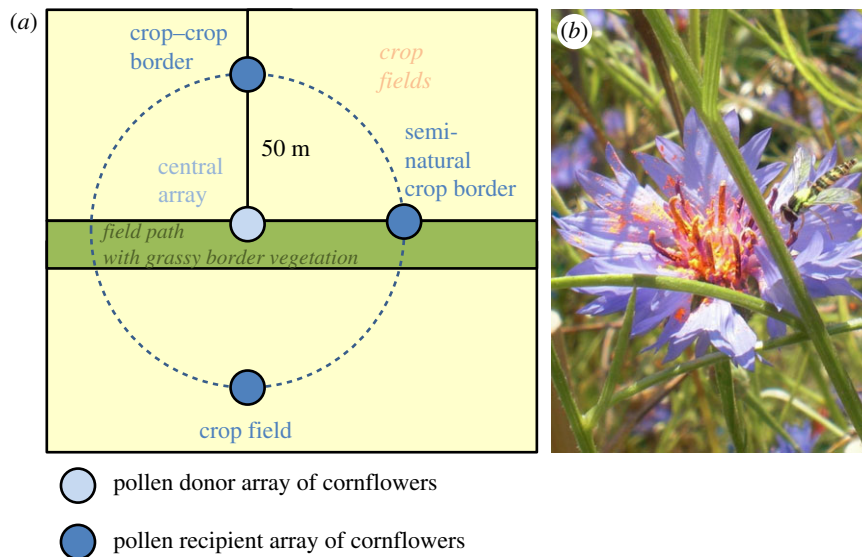


Figure 1. (a) Experimental design of the pollen transfer experiment. At each site three arrays with 10 pots of ‘recipient’ cornflowers were placed at different agricultural border types (crop–crop border or semi-natural crop border) or in a field (crop field). A pollen donor array (with 10 pots of cornflowers) was placed in the centre, at 50 m from the three recipient arrays and was treated with fluorescent dye (b). After 24 h of field exposure 20 flowers from each recipient array were examined for transferred dye. Photo: B. Jünemann. (Online version in colour.)

cyaneus, Asteraceae, obtained from wild populations, Appels Wilde, Germany) along different field borders. Cornflowers are attractive to different bee and hoverfly species [35]. Fluorescent dye has been successfully used to quantify pollen transfer and gene flow among animal-pollinated plants [36,37]. We performed the pollen transfer experiments at six replicated sites in the same study area as the pollinator survey and pollination experiment (above) in Germany. At each site we placed a central array of pollen donor cornflower pots in the semi-natural crop border vegetation next to a field. We then assessed the transmission of fluorescent dye from this donor array to recipient arrays along three different treatments: crop–crop border, semi-natural crop border and crop field treatment (figure 1a). The crop–crop border treatment consisted of a border between two contrasting crops without semi-natural vegetation linking the pollen donor and the recipient array (3 × oilseed rape next to cereal and 3 × spring crops, i.e. sugar beet or maize, next to cereal). In the semi-natural crop border treatment an unpaved roadside with grassy crop border vegetation connected the donor and recipient array. The flower availability of naturally occurring plants in this semi-natural crop border vegetation did not differ among the six sites. Finally, in the crop field treatment we placed the recipient array in a cereal field with no crop border connecting it to the donor array. The three recipient arrays were all placed 50 m from the pollen donor and all experimental cornflowers were clearly visible within the surrounding vegetation.

The experiment was conducted in 2014 in three sites on 18 May and in the three remaining sites on 5 June. On both sampling dates, oilseed rape was no longer flowering. We exposed always 10 pots of cornflowers with comparable flower availability per array in the study sites at least four days before the experiment to make sure that pollinators were aware of the available food resource. Fluorescent dye (RadgloR, Radiant Color, Belgium) was applied to all fresh flowers of the pollen donor arrays (figure 1b) and after 24 h of exposure under warm and sunny conditions, we collected 20 flowers from each of the three recipient arrays per site ($n = 360$ flowers in total). We then assessed if fluorescent dye was present or absent on the stigmas of these flowers using UV light microscopy.

(c) Data analysis

(i) Pollinator survey and pollination experiment

To examine the effects of field border density (configurational heterogeneity) and crop diversity (compositional heterogeneity)

on pollinator abundance, richness and radish seed set, while controlling for the amount of semi-natural cover, we used structural equation models (SEMs). These allowed us to model indirect effects (e.g. of field border density via pollinator abundance on seed set). In particular, we used piecewise SEMs, which allow for a wide range of response distributions in a hierarchical (mixed effects) framework [38]. First we constructed hypothetical models. Then we used the package ‘piecewiseSEM’ to assess the goodness-of-fit based on Shipley’s test of directed separation that combines the p -values of all independence claims in Fisher’s C [39]. To reduce model complexity, we constructed two different hypothetical models comprising either abundance or species richness variables. The first model included effects of local and landscape variables (table 1) on abundance (honeybee, wild bee and hoverfly abundance) and seed set (number of seeds per pod) pooled across transects and surveys, see electronic supplementary material S2, 1.6 for details on model specification and electronic supplementary material, figure S5a). As we expected correlations between honeybee, wild bee and hoverfly abundances we added correlated errors between those variables. Additionally, we included effects of latitude and longitude on bees, hoverflies and seed set, as the geographic position might have a major impact. In the second model (species richness; electronic supplementary material, figure S5b) we included wild bee and hoverfly species richness per field instead of abundance. Here we excluded honeybees as well as the data from the UK, because bee species richness was not available for that country.

All abundance and species richness measures were log transformed, and flower cover was logit transformed to achieve a normal distribution of residuals and better model fit. The variables were then standardized to obtain comparable coefficients. We excluded four extreme outliers from the abundance dataset and two additional ones from the species richness dataset (electronic supplementary material S2, figure S6) as these would have strongly affected the results [40]. Each pathway in the SEM represents a single model for which we used linear mixed-effect models from the package ‘nlme’ [41] with landscape nested in region as a random effect. We also tested whether random intercept or random intercept and slope models were more appropriate (electronic supplementary material S2, 1.6). For the hoverfly abundance model we included crop diversity as random slope, but for all other models we used only random intercept models.

The inclusion of latitude and longitude in the models mainly accounts for the geographic position of regions, but not for the position of landscapes within each region as distances between sites within one region are minimal compared to distances between regions. Therefore, we repeated all analyses with centralized data by standardizing all variables within each region. This resulted in comparable scales of all variables across regions.

All SEMs were manually simplified by removing step-wise pathways with the highest p -value until the best model was found based on the AIC. The residuals of all models were checked for homoscedasticity and normality and we used variance inflation factors (VIFs) in the 'car' package [42] to check for collinearity. All VIFs were <2 [40]. The final models were also checked for spatial autocorrelation of the residuals by using the 'ncf' package [43]. We plotted spline correlograms and did not detect spatial autocorrelation at any distance between our sampling sites.

(ii) Pollen transfer experiment

To compare the pollen transfer among treatments, we examined the probability that pollen had been deposited on a flower of the receiver arrays. We first created a two-column object for the response containing the counts of flowers with fluorescent pollen and without fluorescent pollen per treatment. Second, we fitted a generalized linear-mixed model with binomial errors using the two-column object as the response [44]. This full model contained treatment (crop–crop border, semi-natural crop border or crop field) and crop border type (oilseed rape or spring crop next to cereal) as explanatory variables, and site as random effect. Third, we assessed the significance of pairwise treatment differences using Tukey's contrasts (function 'glht', package 'multcomp' [45]). The reported p -values were adjusted for multiple testing using the single-step method. No overdispersion was detected (dispersion parameter = 0.8, function 'dispersion_glmmer' package 'blmecc' [46]). Homoscedasticity and residual normality were visually checked and no problem was detected. As there was one flower array with very high amounts of fluorescent dye transferred along the crop–crop border, we repeated the analysis by removing all three treatments from the site containing this outlier. As the results were comparable we used the full dataset for interpretation.

3. Results

(a) Pollinator survey and pollination experiment

Overall, we caught 8541 wild bees, 1672 honeybees and 10 715 hoverflies. Most wild bee individuals (excluding UK data and border transects from France) could be identified to species (85%), representing 179 species (electronic supplementary material S2, table S3). However, 2% of all bees could only be identified to morphospecies and 13% were only identified to genus. Almost all hoverfly individuals (99.9%) were identified to species, representing 64 species in total (electronic supplementary material S2, table S4). We collected 7759 pods containing 25 676 seeds from the pollination experiment with radish.

The SEM including pollinator abundance fitted the data well (best simplified model: $C_{10} = 4.31$, $p = 0.933$; figure 2a), and none of the independence claims remained significant indicating that no important links were missing in the model. Results of the best-fitting SEMs are in the electronic supplementary material S2, table S5. The best abundance model revealed that increasing field border density (configurational heterogeneity) had a strong positive effect on wild bee abundance (figures 2a and 3a), but no effect on hoverfly abundance. Conversely, higher crop diversity (compositional

heterogeneity) decreased wild bee abundance (figure 3b). Local flower cover had a weakly negative effect on wild bee and hoverfly abundance, but a positive effect on seed set. Semi-natural cover had a weakly positive effect on hoverfly abundance and a strong positive direct effect on seed set. Seed set was also positively affected by wild bee abundance (figure 3c). However, neither honeybee nor hoverfly abundance influenced seed set. Latitude impacted hoverfly abundance negatively and seed set positively, whereas longitude had a negative effect on seed set.

Replacing abundance by species richness in the SEMs (best simplified model: $C_{14} = 8.79$, $p = 0.844$; figure 2b) resulted in a weakly negative effect of local flower cover on bee richness. Landscape variables had no significant influence on pollinator species richness, but seed set was again enhanced by semi-natural cover in the landscape.

Results of SEMs based on centralized data were similar to those of the first set of analyses (electronic supplementary material S2, table S5, figure S7). However, the effect of field border density was only marginally significant ($p = 0.061$), but similar to the effect size of crop diversity that remained significant ($p = 0.025$; electronic supplementary material, table S5). Additionally, we found a weakly negative effect of crop diversity on hoverfly species richness.

(b) Pollen transfer experiment

Transfer of a pollen analogue from donor to recipient cornflower arrays was about four times higher along crop–crop borders than across crop fields (figure 4; electronic supplementary material S2, table S6; $p = 0.002$) or along semi-natural crop borders ($p = 0.004$). However, crop fields and semi-natural crop borders showed comparable rates of transfer of the pollen analogue from the donor to the recipient array ($p = 0.955$). Results did not change when we excluded the site containing the outlier, but then the difference in transfer of the pollen analogue between crop–crop borders and semi-natural crop borders was only marginally significant. Significantly more pollen analogue was transmitted along borders between oilseed rape and cereal than along borders between spring crops and cereal (electronic supplementary material S2, table S6).

4. Discussion

This study provides three novel key results: First, we found that landscapes with higher field border density had higher wild bee abundance, which translated into increased seed set across four agricultural regions. This suggests a positive, cascading effect of farmland configurational heterogeneity on plant reproductive success. Second, this effect was paralleled by improved transfer of a pollen analogue along crop–crop borders, suggesting that crop–crop borders increase connectivity by facilitating pollinator movement across agricultural landscapes. Third, and surprisingly, increased crop diversity had a consistently negative impact on bee abundance across regions.

(a) Configurational heterogeneity promotes wild bee abundance and pollination services

Our study demonstrates that increased field border density at a landscape scale promotes pollination of plants growing in field borders by enhancing the abundance of wild bees. Higher field

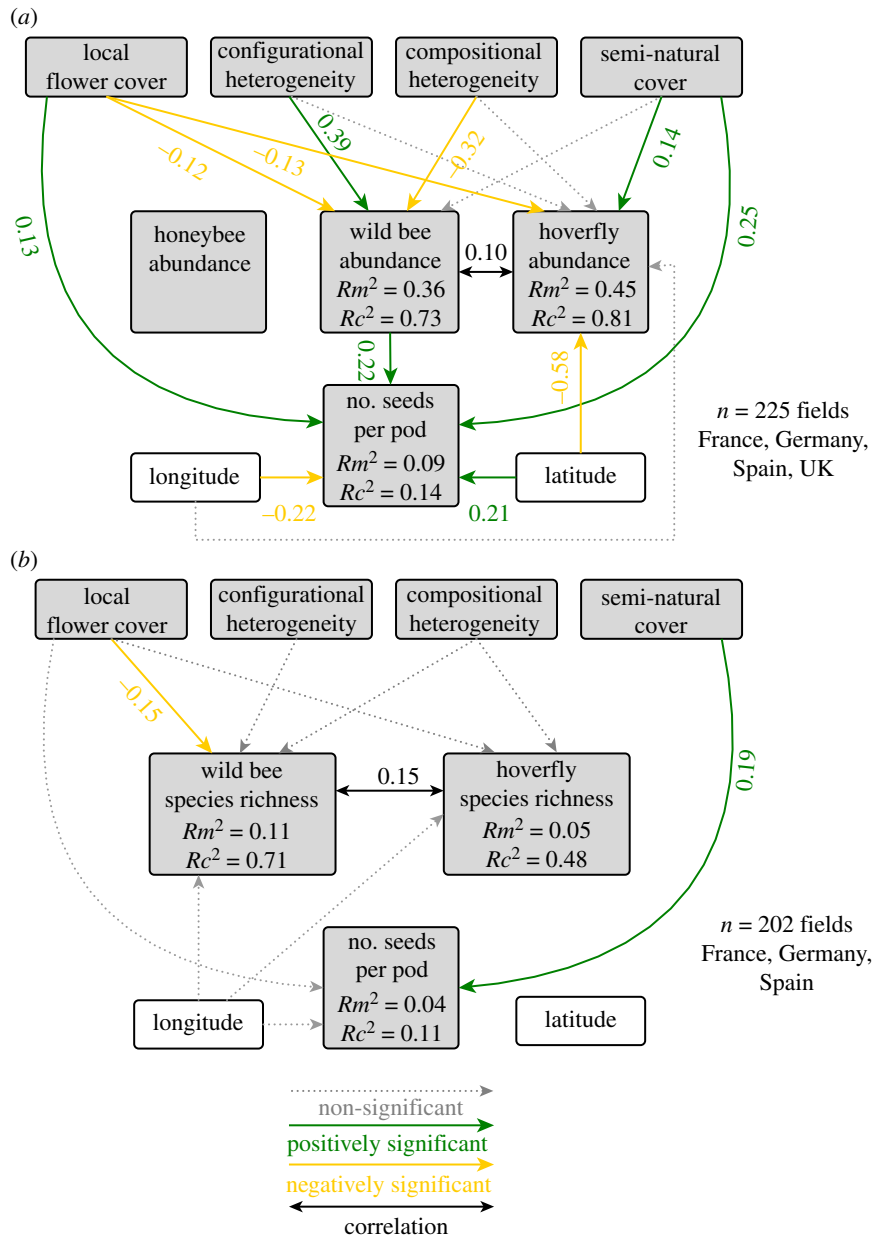


Figure 2. Results of the best piecewise SEMs, based on AIC values analysing the relationship between local flower cover (3 m around pan traps), farmland configurational heterogeneity (field border density), farmland compositional heterogeneity (crop diversity), semi-natural habitat cover, and (a) bee and hoverfly abundances and (b) species richness, and the effects on seed set of potted radish across four countries. Numbers next to arrows show standardized regression coefficients. Latitude and longitude were added as covariates. Conditional (Rc^2 , includes random effects) and marginal (Rm^2 , excludes random effects) R^2 values are presented for response variables. (Online version in colour.)

border density means an increase of border length between directly adjacent crops (crop–crop borders) and borders of fields with semi-natural vegetation (semi-natural crop borders). Semi-natural crop borders are important habitats for pollinators offering nesting sites and food resources [22,47], but the role of crop–crop borders is rarely considered independently of the area of semi-natural crop borders. However, they provide potentially more flowering weeds compared with the field interior due to less intensive management and can be moved much more easily than semi-natural crop borders which are usually permanent habitats. As semi-natural cover had no effect on pollinators in our study, the results indicate a role of different kinds of crop borders independent of the habitat contributed by semi-natural crop borders, probably by promoting pollinator dispersal. The pollen transfer experiment provides novel evidence for improved transmission rates of artificial pollen along crop–crop borders relative to continuous crop fields, demonstrating that crop–crop borders

themselves can guide pollinator movement and may be important for pollinator dispersal. Enhanced connectivity through higher field border density probably leads to higher reproductive success of plant species growing in the field border vegetation. Whether pollinator-dependent crops growing inside the field can also benefit from high configurational heterogeneity remains unclear and should be tested in future studies. However, the low amounts of dye transmitted along semi-natural crop borders were unexpected. This may be due to a dilution effect [48] as pollinators that visited the donor patch could have been attracted to other abundant flowering plants in the semi-natural crop border vegetation, thus hindering dye transmission to our recipient arrays. Additionally, animal movement is usually more tortuous and therefore slower within habitats than between habitats [49].

An alternative explanation for the consistent positive effect of landscape-scale field border density on wild bee abundance and pollination services is that landscapes with

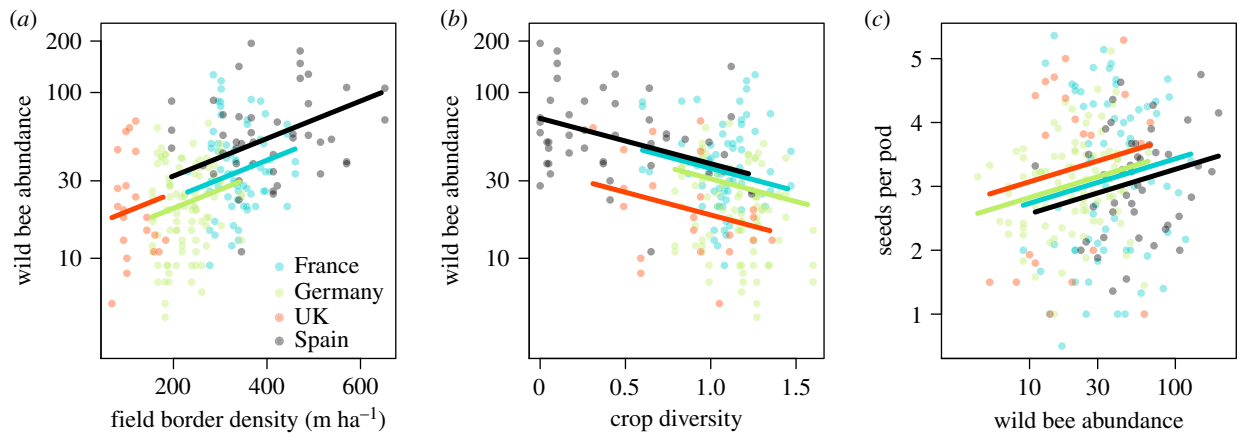


Figure 3. Effects of (a) field border density (configurational heterogeneity) on wild bee abundance ($p < 0.001$), (b) crop diversity (compositional heterogeneity) on wild bee abundance ($p < 0.001$), and (c) wild bee abundance on seed set (mean number of seeds per pod for each field, $p = 0.008$) sampled in crop fields of four countries. Lines show predictions from mixed models using random intercepts for countries. Abundances are shown on a \log_{10} scale. The same relationships were examined in the SEMs (figure 2). (Online version in colour.)

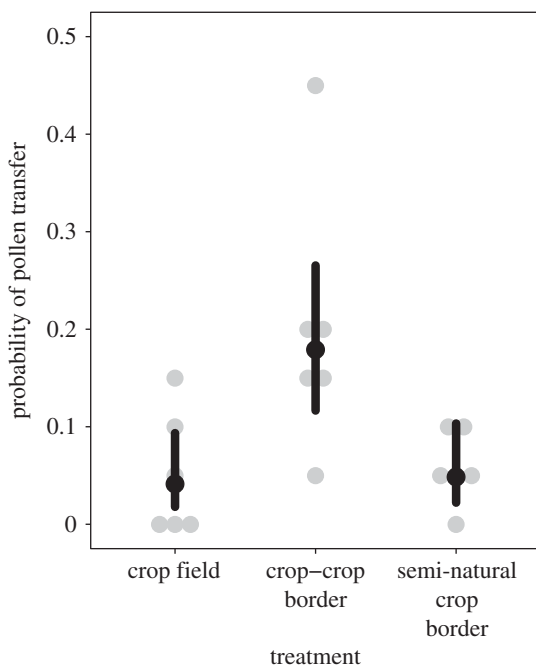


Figure 4. Probability that artificial pollen (fluorescent dye) was transferred from a central donor to flowers of a recipient array 50 m away, along three treatments (crop field, crop-crop border and semi-natural crop borders). Transfer of experimental pollen (fluorescent dye) was significantly higher along crop-crop borders than through crop fields ($p = 0.002$) or along semi-natural crop borders ($p = 0.004$). Treatments were placed in a blocked design (six central donors with three treatments each). For each recipient array, 20 flowers were inspected for fluorescent dye deposition ($n = 360$ flowers in total). Shown are model estimates from generalized mixed models \pm 95% CI (black dots and bars).

higher configurational heterogeneity have enhanced juxtaposition and interspersed of different crop and non-crop cover types and thereby increase resource accessibility to pollinators [15]. However, this hypothesis is not supported by the results for compositional heterogeneity (see below).

The strong importance of farmland configurational heterogeneity for wild bee abundance stands in marked contrast to the weak effect of the configuration of semi-natural cover on pollinators found in previous studies [11,18,19]. The reason for this difference could be that these studies were not designed

to create a gradient in configurational heterogeneity, which was only analysed *post hoc*. Their results, therefore, might reflect a correlation between configurational heterogeneity and some other variable that counteracts its effect; based on our results one such confounding variable might be farmland compositional heterogeneity (see below).

Results based on the centralized dataset show only a marginally significant effect of field border densities. This indicates that the effects within each region are weaker than if we expand the gradient by studying multiple regions. We caution also that, despite the large spatial extent of our study, the results are based on data from only one sampling year. Therefore, more research is needed to confirm that the findings are temporally replicable. Additionally, we did not directly observe pollinator visitation, but measured pollinator abundance indirectly with pan traps which might have caused some bias [50].

(b) Compositional heterogeneity has negative effects on pollinators

A surprising outcome of this study was that, contrary to our expectations, greater crop diversity resulted in decreased bee abundance. One possible explanation would be an unimodal relationship between pollinators and crop diversity and that our landscapes are at the higher range of compositional heterogeneity where we expect a negative trend due to decreasing habitat cover [30]. However, this explanation is unlikely, because our gradient starts at zero (only one crop per landscape; table 1).

An alternative explanation for the negative effect is that crop identity played a major role. We assume that the cover of crops with particularly intensive management increased with crop diversity. For example, crop diversity was associated with high maize cover (electronic supplementary material S2, table S7), which is marked by reduced plant diversity due to higher fertilizer and herbicide inputs compared to cereal crops [51,52]. The low plant diversity of maize fields could explain the apparent negative effect of crop diversity on bee abundance, although maize was widespread only in France and Germany. Indeed, an additional analysis supported the negative impact of maize cover on bee abundance in these two countries (electronic supplementary material S2, figure S8). The explanation that high crop diversity was associated with a high proportion of

mass-flowering crops distracting pollinators from our traps [53] is unlikely, as most experiments were conducted after oilseed rape bloom. However, the reason for the negative effect of crop diversity on bees in all countries cannot be identified conclusively based on our dataset, because the study was not designed to test for impacts of certain crop types which differed between countries (electronic supplementary material S2, table S1) and there were multiple correlations among them. To disentangle the effects of farmland compositional heterogeneity from specific crop types studies designed to answer this question are needed.

Apart from a weak decrease of hoverfly species richness with crop diversity in the model based on centralized data which might also be due to increased cover of crops with unfavourable management, hoverflies were not affected by any landscape variables in our analysis. The reason might be that cereals were the main crop in all our regions (electronic supplementary material table S1 and S7). Cereals support high densities of aphids [54]. Therefore, food availability might have been high in all landscapes for the dominant, aphid-feeding hoverfly species in our study (*Eupeodes corollae*, *Episyrphus balteatus* and *Sphaerophoria scripta*), which accounted for 89% of all hoverfly individuals captured.

(c) Semi-natural cover has no effect on pollinators

The area of semi-natural cover including non-forest cover types (e.g. semi-natural grasslands) and linear crop borders (grassy, woody and bare ground) had only a weakly negative effect on hoverfly abundance, but no significant effect on bee abundance or species richness. The generally low amount and variability of non-forest semi-natural cover across regions due to our study design (mean \pm s.e. of $5.08 \pm 0.14\%$) may not have provided sufficient variation in semi-natural cover among landscapes to detect this effect. Studies showing significant effects of semi-natural cover usually encompass larger gradients, at least between 1% and 30% [17,55]. However, we found a direct positive influence of semi-natural cover on seed set of radish, which was not mediated by any pollinator group. It is possible that other insects than bees and hoverflies contributed to radish pollination (e.g. other Diptera have been reported to visit radish [56]), albeit this explanation is unlikely as these insects usually depend less on semi-natural cover [57]. Alternatively, biological control of pest species attacking radish may play an important role in enhancing radish seed set. For example, flower damage by pollen beetles and their larvae (*Meligethes aeneus*) can substantially reduce seed production in Brassicaceae [58]. Pollen beetles are attacked by a number of parasitoid species that positively respond to semi-natural cover [59], suggesting that higher parasitism rates could be responsible for enhanced seed set in landscapes with high proportions of semi-natural cover. These parasitoids depend on

nectar resources which could also explain the positive effect of flower cover on seed set.

5. Conclusion

Our study demonstrates that the heterogeneity of the crop production area is an important, hitherto little investigated factor for pollinator communities in agricultural landscapes. Based on our finding of enhanced wild bee abundance and plant reproductive success in landscapes with high configurational heterogeneity, we recommend promoting field borders and reversing the current trend of increasing field sizes. We demonstrate that even crop–crop borders without semi-natural vegetation enhance pollinator movement and thereby landscape connectivity. However, our results indicate that major increases of field border densities may be necessary to promote wild bee abundances within a region.

Additionally, we show that policies aimed to increase crop diversity are not always positive for pollinators and may even have negative effects if the increase in crop diversity is driven by crop types under intense management such as maize. Therefore, it is essential to consider crop identity and farming practices in these policies. We conclude that enhancing configurational heterogeneity combined with the reduction of crop areas with particularly intensive management could be a promising tool for supporting pollinators and pollination services in future agricultural landscapes.

Data accessibility. All datasets and R codes used for the analyses of this article have been uploaded as part of the electronic supplementary material S3 and S4.

Authors' contributions. A.L.H., U.G.K., T.T., P.B. and Y.C., as well as C.S., L.F., J.-L.M., J.B., L.B., F.B. and G.S., developed the conceptual foundations for this manuscript. A.L.H., U.G.K., A.B.B., C.B., R.G., D.G. and G.S. performed the field surveys and A.L.H., J.B., M.A.M.-G. and A.R. identified species. C.S. compiled data and A.L.H. and U.G.K. performed the analyses with the support of P.B. A.L.H. wrote the first draft of the manuscript. All authors contributed substantially to revisions.

Competing interests. We declare we have no competing interests.

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