Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions

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Agricultural landscape homogenization has detrimental effects on biodiversity and key ecosystem services. Increasing agricultural landscape heterogeneity by increasing seminatural cover can help to mitigate biodiversity loss. However, the amount of seminatural cover is generally low and difficult to increase in many intensively managed agricultural landscapes. We hypothesized that increasing the heterogeneity of the crop mosaic itself (hereafter "crop heterogeneity") can also have positive effects on biodiversity. In 8 contrasting regions of Europe and North America, we selected 435 landscapes along independent gradients of crop diversity and mean field size. Within each landscape, we selected 3 sampling sites in 1, 2, or 3 crop types. We sampled 7 taxa (plants, bees, butterflies, hoverflies, carabids, spiders, and birds) and calculated a synthetic index of multitrophic diversity at the landscape level. Increasing crop heterogeneity was more beneficial for multitrophic diversity than increasing seminatural cover. For instance, the effect of decreasing mean field size from 5 to 2.8 ha was as strong as the effect of increasing seminatural cover from 0.5 to 11%. Decreasing mean field size benefited multitrophic diversity even in the absence of seminatural vegetation between fields. Increasing the number of crop types sampled had a positive effect on landscape-level multitrophic diversity. However, the effect of increasing crop diversity in the landscape surrounding fields sampled depended on the amount of seminatural cover. Our study provides large-scale, multitrophic, cross-regional evidence that increasing crop heterogeneity can be an effective way to increase biodiversity in agricultural landscapes without taking land out of agricultural production.

multitaxa | biodiversity | crop mosaic | farmland | landscape complementation

Agriculture dominates the world's terrestrial area (1). Agricultural landscape homogenization through the decrease of seminatural cover, crop specialization, and field enlargement (2–4) represents a continuing worldwide threat to biodiversity and the delivery of key ecosystem services to people (5). There is ample evidence that enhancing landscape heterogeneity by reversing

Significance

Agricultural landscape homogenization is a major ongoing threat to biodiversity and the delivery of key ecosystem services for human well-being. It is well known that increasing the amount of seminatural cover in agricultural landscapes has a positive effect on biodiversity. However, little is known about the role of the crop mosaic itself. Crop heterogeneity in the landscape had a much stronger effect on multitrophic diversity than the amount of seminatural cover in the landscape, across 435 agricultural landscapes located in 8 European and North American regions. Increasing crop heterogeneity can be an effective way to mitigate the impacts of farming on biodiversity without taking land out of production.

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the decline in seminatural cover can benefit biodiversity in agricultural landscapes (6–8). However, the amount of seminatural cover keeps decreasing in many agricultural landscapes, and the efficiency of policies focusing solely on maintaining or increasing seminatural cover has been questioned (9).

While half of the biodiversity in agricultural landscapes occurs exclusively in seminatural cover (10), the crop mosaic offers a wide range of resources to the other half, including to species occurring exclusively in crop fields and providing key ecosystem services, such as crop pollination or biological pest control (11, 12). It is therefore of increasing interest to evaluate whether enhancing landscape heterogeneity by increasing the heterogeneity of the crop mosaic itself (hereafter "crop heterogeneity") can also benefit biodiversity (Fig. 1). There is growing pressure on agricultural land for food and energy production as well as for urbanization. Therefore, measures to benefit biodiversity consisting of a rearrangement of the production area, as opposed to measures focusing solely on its reduction, could provide valuable new sustainable policy options.

Crop heterogeneity can be decomposed into compositional heterogeneity, i.e., the composition of the crop mosaic (e.g., crop diversity), and configurational heterogeneity, i.e., the shape and spatial arrangement of fields (e.g., mean field size, ref. 13; see further explanation in *Methods*). These 2 components of crop heterogeneity may influence farmland biodiversity in several ways (see detailed alternative hypotheses in *SI Appendix*, section 1). First, increasing crop diversity may benefit biodiversity if many species are specialists of distinct crop types (i.e., habitat specialization; Hyp-1a in *SI Appendix*, section 1; ref. 14). In that case, sampling increasing numbers of crop types should lead to observing increasing levels of species diversity. Second, increasing crop diversity may also benefit biodiversity through a landscape-level effect if many species require multiple resources provided by different crop types (i.e., landscape complementation; Hyp-1b in *SI Appendix*, section 1; ref. 15). In that case, sampling a given number of crop types surrounded by increasing levels of crop diversity available in the landscape should lead to observing increasing levels of species diversity. Third, decreasing mean field size may benefit biodiversity through a landscape-level effect if small fields provide easier access to adjacent crop fields for many species (i.e., landscape complementation; Hyp-2a in *SI Appendix*, section 1; refs. 15 and 16). In that case, sampling a given number of fields surrounded by fields with decreasing mean sizes should lead to observing increasing levels of species diversity.

Biodiversity responses to crop heterogeneity may be nonlinear and nonadditive. For instance, increasing the diversity of crops available in the landscape may benefit biodiversity in a given field only if fields are small enough for adjacent fields to be reached easily. Additionally, the effects of increasing crop heterogeneity on biodiversity may depend on the amount of seminatural cover in the landscape. For instance, the "intermediate landscape-complexity" hypothesis (17) predicts that the positive biodiversity-crop heterogeneity relationship is stronger in landscapes with intermediate amounts of seminatural cover (e.g., 5–20%) than in landscapes with little (e.g., <5%) or much seminatural cover (e.g., >20%; ref. 6). Sampling over a wide range of landscapes may therefore be necessary to understand the general effect of crop heterogeneity on farmland biodiversity.

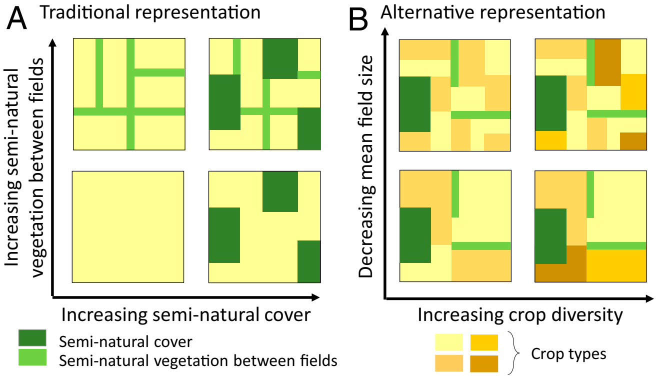

Fig. 1. (*A*) Traditional and (*B*) alternative representations of agricultural landscape heterogeneity, focusing either on seminatural heterogeneity or crop heterogeneity, are associated with distinct hypotheses (see details in *SI Appendix*, section 1; large squares represent landscapes). Adapted with permission from ref. 13.

The biodiversity–crop heterogeneity relationship may vary among taxa (e.g., ref. 18). For instance, it may be more positive for species and taxa that have lower habitat area requirements (e.g., small species; ref. 19) or higher habitat specialization levels (e.g., ref. 20). Although in-depth understanding of the effects of crop heterogeneity on each species or taxon is valuable, it is also critical to develop environmental policies that are effective across a wide range of species (21). To achieve this, we here use a cross-regional sampling scheme in Europe and North America and a synthetic index integrating information on multiple trophic groups to identify landscape patterns that simultaneously increase the diversity of most taxa (22).

We selected 435 landscapes along orthogonal gradients of mean size and diversity of crop types available in the landscape in 8 contrasting agricultural regions in France, the United Kingdom, Germany, Spain, and Canada (Fig. S2.1, *SI Appendix*, section 2). In each landscape, we selected 3 sampling sites in 1, 2, or 3 crop types. We sampled 7 taxa representing a wide range of ecological traits, functions, and trophic levels (plants, bees, butterflies, hoverflies, carabids, spiders, and birds) in each field. We then computed a synthetic index of multitrophic diversity (*Methods*). We tested the relative effects of mean field size, the number of crop types sampled, the diversity of crop types available in the landscape, and the amount of seminatural cover in the landscape on multitrophic diversity and on the species richness of taxonomic groups. We also evaluated whether the effects of mean field size and the diversity of crop types available in the landscape were nonlinear, nonadditive, and influenced by seminatural cover (see detailed hypotheses in *SI Appendix*, section 1).

Results and Discussion

Our study provides large-scale evidence that crop heterogeneity is a major driver of multitrophic diversity in agricultural landscapes. The number of crop types sampled in the landscape, and the mean size and diversity of crop types available in the landscape were consistently included in all models (Fig. 2*A*). Together, they accounted for 61% of the explained variance in multitrophic diversity, while seminatural cover accounted for 24% (Fig. 2*B*). Interactions between seminatural cover and mean size/crop diversity of fields available in the landscape also accounted for an important part of the explained variance (15%), indicating that the effects of crop heterogeneity were modulated by the amount of seminatural cover in the landscape (Fig. 3). The effects of crop heterogeneity on multitrophic diversity were consistent across the 8 European and North American regions (Fig. 4). The effects of crop heterogeneity on the species richness of taxonomic groups were similar to their effects on multitrophic diversity and similar across the 7 taxa (Fig. 5 and Fig. S5.2, *SI Appendix*, section 5). They hold true when considering either landscape-level or field-level multitrophic diversity, including when focusing only on cereal fields, the most dominant crop type across our 8 regions (Table S5.11, *SI Appendix*, section 5). Their effects were also unchanged when potential confounding factors such as the identity of crop types sampled, land-use intensity within fields sampled (i.e., an index combining data on plowing, fertilizer, herbicide, and insecticide), the composition of the crop mosaic, grassland cover, or hedgerow length available in the landscape were taken into account in our analyses (*SI Appendix*, section 5).

Consistent Positive Effects of Decreasing Mean Field Size on Multitrophic Diversity.

Decreasing mean field size was the main driver of multitrophic diversity variations, mean field size and mean field size^2 together accounting for 47.4% of the explained variance in

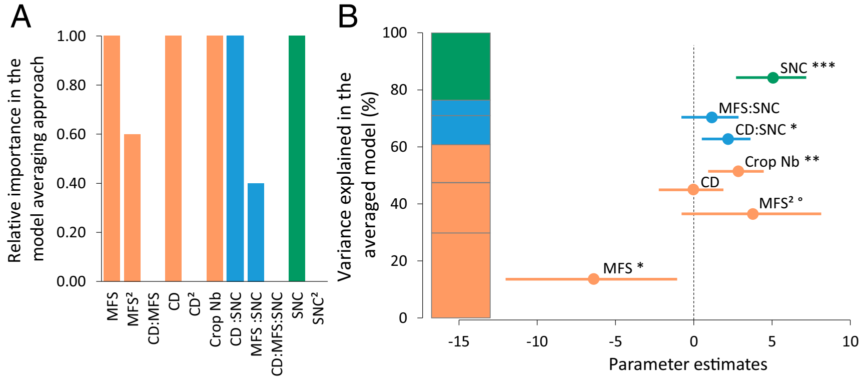

Fig. 2. (*A*) Importance and (*B*) relative effect of the CD, the number of crop types sampled (Crop Nb), MFS, SNC, and interaction terms (CD:SNC, MFS:SNC) on multitrophic diversity. $P < 0.1$; $*P < 0.05$; $**P < 0.01$; $***P < 0.001$. Variables are grouped in 3 components: orange = crop heterogeneity (MFS, MFS^2, CD, CD^2, MFS:CD, Crop Nb), green = SNC (SNC, SNC^2), blue = interactive effects between crop heterogeneity and SNC (CD:SNC, MFS:SNC, CD:MFS:SNC). The relative importance of variables is estimated as the proportion of submodels where the variable was selected. The variance explained by each variable corresponds to the ratio between its parameter estimate and the sum of all parameter estimates based on a model averaging approach applied to model 1.

multitrophic diversity (Fig. 2*B*). The effect of decreasing mean field size from 5 to 2.75 ha was as strong as the effect of increasing seminatural cover from 0.5 to 11% of the landscape (Fig. 3*B*). Such a positive effect of decreasing mean field size on multitrophic diversity is consistent with the hypothesis that smaller fields provide easier access to multiple cover patches, in particular for species that require resources occurring in different cover types (landscape complementation; refs. 15 and 16). The positive effect of decreasing mean field size was particularly clear and strong when mean field size fell below 6 ha (93% of landscapes studied).

Although the strength of this effect varied significantly among regions, decreasing mean field size had a consistent positive effect across all regions studied (Fig. 4 and *SI Appendix*, section 5). It was also consistently positive across all taxa considered separately, from primary producers to predators (Fig. 5 and *SI Appendix*, section 5). Previous studies have already reported positive effects of decreasing mean field size on the diversity of several taxa considered separately (e.g., refs. 23–27). Our study, based on multiple regions and multiple trophic groups, shows that the benefits of decreasing mean field size can be generalized to multitrophic diversity across a wide range of agricultural regions.

Previous studies suggested that the positive effect of decreasing mean field size on multitrophic diversity may be primarily due to the presence of seminatural vegetation between fields (e.g., refs. 23, 25, and 26). To test this hypothesis, we selected a subset of landscapes for which mean field size and the length of seminatural vegetation between fields were uncorrelated (*SI Appendix*, section 5). The analysis, based on 274 landscapes, showed that the positive effect of increasing mean field size on multitrophic diversity cannot be explained solely by the increase in the length of seminatural vegetation between fields. Increasing the length of seminatural vegetation between fields had a positive effect on multitrophic diversity but including this effect in our model did not change the effect of mean field size on multitrophic diversity (Table S5.8, *SI Appendix*, section 5). This result suggests that smaller fields benefit multitrophic diversity even in the absence of seminatural vegetation between fields.

Finally, the presence of the interaction term between mean field size and seminatural cover in our model (Fig. 2*A*) suggests that the effect of mean field size on multitrophic diversity tends to be modulated by the amount of seminatural cover available in the landscape (Fig. 3*B*). To further explore this interaction, we used a moving window modeling approach (ref. 28; *SI Appendix*, section 5). This analysis confirmed that decreasing mean field size had a consistent positive effect on multitrophic diversity along the gradient of seminatural cover. Moreover, it suggested that this effect is stronger when seminatural cover is below 8%, i.e., when seminatural cover is too scarce to provide access to the multiple resources required by most species occurring in agricultural landscapes (Fig. S5.5.B, *SI Appendix*, section 5).

Complex Effects of Increasing Crop Diversity on Multitrophic Diversity. The number of crop types sampled in each landscape and the diversity of crop types available in the landscape surrounding sampled fields were consistently included in all models (Fig. 2*A*). This result suggests that both field-level (i.e., habitat specialization) and landscape-level processes (i.e., landscape complementation and/or spill-over) can contribute to the effect of crop diversity on multitrophic diversity (*SI Appendix*, sections 1 and 4).

Increasing the number of crop types sampled had a significant positive effect accounting for 13% of the explained variance in landscape-level multitrophic diversity (Fig. 2*B*). This result confirms that increasing crop diversity results in a larger number of distinct habitats, and therefore higher biodiversity levels by increasing the number of specialist species in the landscape (Hyp-1a in *SI Appendix*, section 1; ref. 20).

The main effect of increasing the diversity of crop types available in the landscape was nonsignificant but significantly mediated by seminatural cover. These effects were similar across all regions (Fig. 4). Together, the diversity of crop types available in the landscape and its interaction with seminatural cover accounted for 10% of the explained variance in multitrophic diversity (Fig. 2*B*). The landscape-level effect of increasing crop diversity on multitrophic diversity ranged from negative in landscapes with low seminatural cover to positive in landscapes with high seminatural cover (Fig. 3*A*). This result is consistent with the variability of effects observed across previous studies (e.g., refs. 23, 29, and 30). To further explore this interaction, we used the same moving window modeling approach described above (*SI Appendix*, section 5). This analysis confirmed that the landscape-level effect of increasing crop diversity on multitrophic diversity was positive in landscapes with more than 11% seminatural cover (i.e., 50% of landscapes included in our study), nonsignificant in landscapes with 4–11% seminatural cover (i.e., 34% of landscapes), and negative in landscapes with less than 4% seminatural cover (i.e., 16% of landscapes; Fig. S5.5.A, *SI Appendix*, section 5).

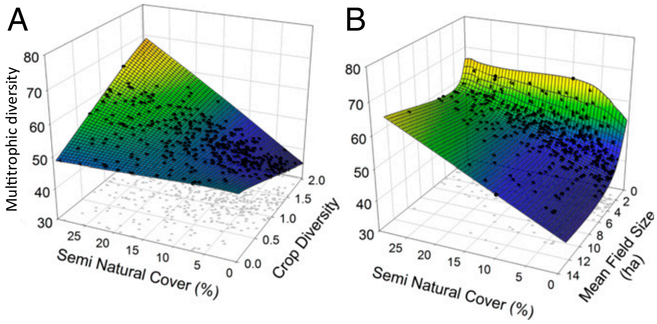

Fig. 3. Interactive effects of (*A*) CD and SNC and (*B*) MFS and SNC on multitrophic diversity. The color gradient corresponds to multitrophic diversity values, ranging from low values (blue) to high values (red). Slopes are based on the outputs of model 1 (see *Methods*). Gray dots show the overall gradients in CD, MFS, and SNC across the 435 landscapes located in 8 regions.

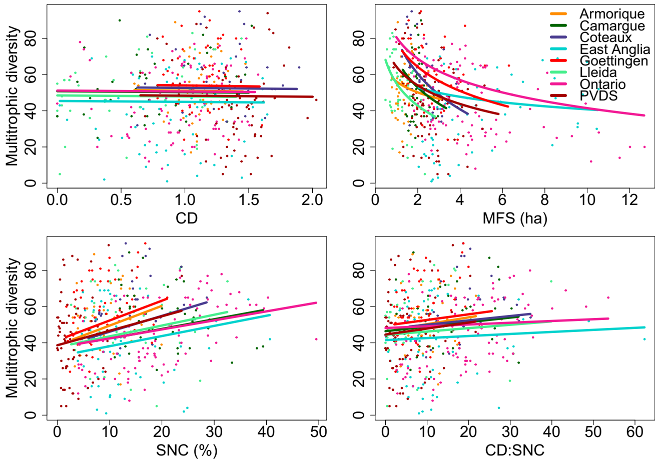

Fig. 4. Effects of CD, MFS, SNC, and the interaction between CD and SNC (CD:SNC) on multitrophic diversity in different regions. Slopes are based on the outputs of model 2 (see *Methods*) including a random effect of region on these 4 slopes (n = 435 landscapes). Colors indicate the region.

The positive landscape-level effect of increasing crop diversity on multitrophic diversity observed in landscapes with more than 11% seminatural cover supports the "landscape complementation" hypothesis (Hyp-1b in *SI Appendix*, section 1). This finding is consistent with the fact that a diverse crop matrix provides a temporal continuity of food sources (31) while seminatural patches provide stable resources, for example, for nesting or shelter (e.g., ref. 32). Such complementation among multiple cover types has been described for several species (e.g., refs. 33 and 34). Our study, based on multiple regions and multiple trophic groups, shows that the positive landscape-level effect of increasing crop diversity can be generalized to multitrophic diversity across many agricultural landscapes (50% of landscapes included in our study).

The negative landscape-level effect of increasing crop diversity on multitrophic diversity in landscapes with less than 4% seminatural cover supports the "minimum total habitat area requirement" hypothesis (Hyp-1c in *SI Appendix*, section 1). This finding is consistent with the fact that landscape simplification tends to filter out species with large body sizes (35), which also have high minimum total habitat area requirements (36), and may therefore require high amount of a single crop type. However, taxa included in the present study were associated with a wide range of ecological traits, and therefore a wide range of minimum total habitat area requirements. That they showed a consistent response to crop diversity and the interaction of crop diversity and seminatural cover (Fig. 5) suggests that the minimum total habitat area requirement hypothesis is unlikely to be the sole mechanism contributing to our results. Future research is needed to identify additional mechanisms and conditions under which increasing crop diversity leads to a consistent net positive effect on multitrophic diversity, i.e., a positive effect of habitat specialization plus landscape complementation processes.

Implications for Agricultural Policies. Our study has important implications for large-scale policy schemes implemented across a wide range of contexts such as the European Common Agricultural Policy and its recent greening (21), the Canadian Agriculture Policy Frameworks (37), or the United States Farm Bill (38).

First, our results suggest that increasing crop heterogeneity may have a similar or greater benefit for multitrophic diversity to increasing seminatural cover (Fig. 2*B*) or even decreasing field-level land-use intensity (ref. 16; Table S5.12, *SI Appendix*, section 5). Given current challenges to increase seminatural cover and limit chemical use in agricultural landscapes (39), policies aiming at increasing crop heterogeneity may represent an effective and complementary way to improve biodiversity conservation in agricultural landscapes. Policy measures favoring crop heterogeneity may be more easily implemented than policies to increase seminatural cover or reduce chemical use (40). Associated with adequate economic incentives, they may also be more favorably perceived by farmers and thus lead to higher uptake than measures requiring farmers to take land out of production (39). Such measures may also contribute to the development of frameworks that reward farmers for sustainable land stewardship.

We observed a consistent effect of crop heterogeneity on species diversity across 7 taxa representing a wide range of ecological traits, functions, and trophic levels (plants, bees, butterflies, hoverflies, carabids, spiders, and birds; Fig. 5). We observed landscapes where 6 or even all 7 taxa reached the threshold of 60% of the maximum species richness observed within a given region (Fig. 4). Our study therefore suggests that policies to increase crop heterogeneity would be an effective way to increase the diversity of all components of biodiversity simultaneously and restore multitrophic biodiversity in agricultural landscapes.

Finally, our results can contribute to the development of policies adapted to different landscape contexts. For instance, our results suggest that policy measures aimed at decreasing field sizes to below 6 ha may be particularly effective to promote multitrophic diversity in agricultural landscapes, especially in landscapes where seminatural cover is below 8%. Our results also caution against a "blind" increase of crop diversity. Measures aimed at increasing crop diversity may be effective to promote multitrophic diversity in landscapes where seminatural cover exceeds 11%. However, they are more likely to be effective in promoting multitrophic diversity across all agricultural landscapes if combined with measures promoting the restoration or maintenance of seminatural cover.

Conclusion

Our study demonstrates the importance of crop heterogeneity for multitrophic diversity in agricultural landscapes: The effect of maintaining/increasing crop heterogeneity is likely to be as important as the effect of maintaining/increasing seminatural cover. This finding suggests that field enlargement and crop specialization, especially the former, have been underestimated drivers of past and ongoing biodiversity declines. More importantly, our study shows that increasing crop heterogeneity represents a major potential lever to increase synergies between food production and biodiversity conservation.

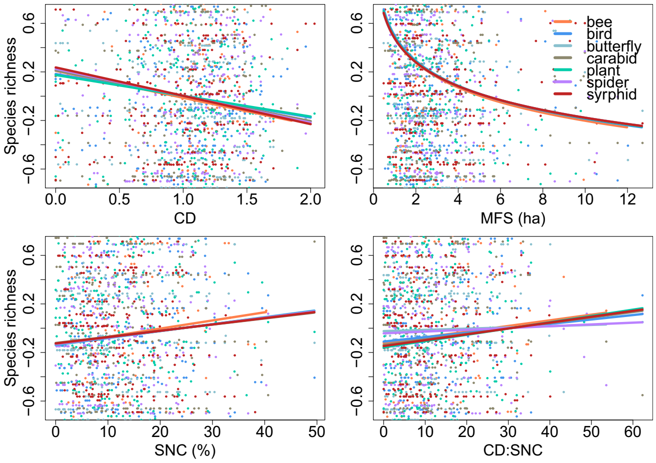

Fig. 5. Effects of CD, MFS, SNC, and the interaction between CD and SNC (CD:SNC) on the landscape-level species richness of taxonomic groups. Slopes are based on the outputs of model 10 (see *SI Appendix*, section 5) including a random effect of taxon on these 4 slopes (n = 435 landscapes). Colors indicate the taxon.

Methods

Region, Landscape, and Sampling Site Selection. We selected 8 agricultural regions (Armorique, Camargue, Coteaux de Gascogne, and Plaine et Val de Sèvre in France, East Anglia in the United Kingdom, Goettingen in Germany, Lleida in Spain, and Eastern Ontario in Canada; Fig. S2.1, *SI Appendix*, section 2) belonging to 6 different ecoregions (41) and differing in topography, climate, field shapes, and agricultural cover types and products (e.g., rice, dairy, tree crops).

We used the best spatial data available within each region before field work to identify all 1 km × 1-km rural landscapes, i.e., those dominated by agricultural cover (>60%, including all crops and grassland managed for agricultural production). We then developed a protocol to select a combination of landscapes that maximized the gradients of crop diversity and mean field size, while minimizing the correlation between them (42). Crop diversity may theoretically be constrained by the number and size of fields in landscapes with large fields. However, in our dataset, mean field size was smaller than 12 ha and was therefore not a limiting factor for crop diversity within the 1 km × 1-km landscapes. We selected between 32 and 93 landscapes within each region, totaling 435 landscapes across all regions.

We selected 3 sampling sites within each landscape, totaling 1,305 sampling sites across all regions. The number of crop types sampled ranged from 1 to 3 per landscape. Where feasible, we located sampling sites in dominant agricultural cover types within each region (e.g., wheat fields and oilseed rape in Goettingen). When this was not feasible, we located sampling sites in agricultural cover types that were accessible within a given landscape (*SI Appendix*, section 3). The 3 sampling sites were at least 200 m from each other, at least 50 m from the border of the landscape, and at least 50 m from patches of nonagricultural cover types such as forests and urban areas.

Multitaxa Sampling. We selected 7 taxa representing a wide range of ecological traits, functions, and trophic levels which, combined into a multidiversity index (see below), represent a proxy for multitrophic diversity: plants, bees, butterflies, hoverflies, carabids, spiders, and birds. All taxa were sampled using standardized sampling protocols across all regions, allowing us to test the consistency of effects across the 8 regions (*SI Appendix*, section 3).

At each sampling site, we selected 2 parallel 50-m "transects," one located at the field edge and the other inside the field 25 m away from the first transect (Figs. S3.1 and S3.2, *SI Appendix*, section 3). Birds were sampled using point counts centered on the field-edge transect. Plants were surveyed along both transects. Butterflies were surveyed visually using timed walks along both transects. Bees and hoverflies were sampled using colored pan traps on poles erected at each end and in the center of all transects. Carabids and spiders were sampled using pitfall traps installed at each end of all transects. Captured arthropods were preserved in ethanol prior to identification. Multiple survey visits were conducted during the season when relevant (*SI Appendix*, section 3). Each landscape was sampled during 1 y and sampling of landscapes was distributed across 2 y within each region, between 2011 and 2014 (Table S3.1, *SI Appendix*, section 3).

We identified more than 167,000 individuals from 2,795 species (Table S3.2, *SI Appendix*, section 3). For each taxon, we calculated species richness at the landscape level, i.e., across all 3 sampling sites and across all visits when multiple survey visits were conducted. The average species richness per landscape varied greatly among taxa, from 5.4 for butterflies to 44.9 for plants. Correlations in average species richness between pairs of taxa were weak (<0.41), with an average correlation of 0.07 (Table S3.3, *SI Appendix*, section 3).

Multitrophic Diversity Index. A classical approach in the literature consists of calculating the average, standardized diversity across taxa (43). However, this approach has limitations (*SI Appendix*, section 3). Although very high/low values imply that all taxa exhibit high/low diversity, intermediate values are difficult to interpret as they may correspond to situations where 1) diversity values are intermediate for all taxa, or 2) diversity values are high for some taxa and low for others, i.e., trade-offs among taxa. To overcome this limitation, we used a threshold approach initially developed to aggregate multiple ecosystem functions (22).

For each taxon and each region, we identified the maximum species richness observed across all landscapes. We used the 95th percentile as the maximum observed species richness (hereafter "SR max") to minimize the effect of outliers. Next, we identified which landscapes attained a given threshold (x) of SR max. We chose to use an intermediate threshold of 60% because intermediate thresholds have been shown to provide an effective measure of multitrophic diversity in agricultural landscapes (ref. 43 and *SI Appendix*, section 3). We then tallied the proportion of taxa that exceeded the given threshold to produce a multidiversity index (T60.landscape) for each landscape, based on the following formula:

$$\mathrm{Multidiversity(Tx.\,landscape)} = \frac{1}{n}\sum_{i=1}^{i=n}[\mathrm{SR}\ i > (x \times \mathrm{SR\ max.\,region\ j})],$$

where n is the number of taxa for which data were available in a given landscape (*SI Appendix*, section 3), SR_i is the number of species for taxon i, x is the minimum threshold to be reached, and SRmax.region j is the maximum species richness for taxon i in the region the landscape considered belonging to. This multidiversity index ranges between 0 and 1 (*SI Appendix*, section 3). For simplicity, we hereafter refer to "landscape-level multitrophic diversity" rather than T60.landscape.

Mean Field Size and Diversity of Crop Types in the Landscape. We used a standardized protocol across all regions to produce land-cover maps allowing us to compare consistency of effects across the 8 regions (*SI Appendix*, section 4). We conducted extensive ground-truthing surveys during the field seasons to map all fields, linear elements between adjacent fields, and nonagricultural covers. We built a common land-cover classification for the 8 regions (*SI Appendix*, section 4). We then used these standardized, detailed maps to calculate 4 explanatory variables for each landscape: diversity of crop types in the landscapes, mean field size, seminatural cover, and total length of seminatural linear elements between fields.

We calculated the Shannon diversity of agricultural cover types (hereafter "the diversity of crop types in the landscape;" CD) and the mean field size in hectares (MFS). Neither CD nor MFS was correlated with local land-use intensity (an index combining data on plowing, fertilizer, herbicide, and insecticide) or the overall composition of the crop mosaic across all regions (*SI Appendix*, section 5). CD and MFS were moderately correlated with the type of crops sampled in some regions and MFS was moderately correlated with the proportion of grassland in the crop mosaic, but none of these correlations affected our conclusions (*SI Appendix*, section 5). We calculated the percentage of seminatural cover types, i.e., woodland, open land, and wetland (SNC), in each landscape. We also calculated the total length of linear seminatural elements between fields, e.g., hedgerows, grassy margins (SNL; measured in meters). SNL and MFS were highly correlated in some regions (Table S5.6, *SI Appendix*, section 5). As a result, we did not include SNL in the main analyses and only tested the relative effect of MFS and SNL using a subset of our dataset for which MFS and SNL were not strongly correlated (*SI Appendix*, section 5).

Data Analysis. We first tested the effect of crop heterogeneity on multitrophic diversity (model 1). We fitted a linear mixed model with restricted maximum likelihood using the landscape-level multidiversity index (T60.landscape) as the response variable. We included the number of crop types sampled per landscape (CropNb), CD, MFS, and SNC as explanatory variables (see alternative hypotheses in *SI Appendix*, section 1). We included both interaction effects and quadratic effects. Due to a positive skew in the distribution of MFS, we used log MFS in all analyses. To reflect the large-scale spatial and temporal structure of our dataset, we added sampling year (Year), nested within study region (Region), as a random effect. To reflect the spatial structure of our dataset within each region, we included the longitude and latitude of the center of each landscape (Lat, Lon) as covariates. We standardized all fixed effects to allow for a direct comparison of estimates.

*Model 1: lmer (T60.landscape ∼ CD * MFS * SNC +* CD^2 *+* MFS^2 *+* SNC^2 *+ CropNb + Lat + Lon + (1|Region/Year)).* Then, we added random effects for region on the slopes of the diversity of crop types in the landscape, MFS, SNC, as well as the interaction between the CD and SNC (model 2). We assumed that the effects of region on the intercept and slopes were uncorrelated. To test whether region had a significant effect on the slope of either the CD, MFS, or SNC, as well as the interaction between crop diversity and SNC, we used the function exactRLRT from package RLRsim.

*Model 2: lmer (T60.landscape ∼ CD * MFS * SNC +* CD^2 *+* MFS^2 *+* SNC^2 *+ CropNb + Lat + Lon + (1|Region/Year) + (0+CD|Region)) + (0+MFS|Region) + (0+SNC|Region) + (0+CD:SNC|Region)).* We then tested the effects of crop heterogeneity on the SR of taxonomic groups (model 3). To do this, we fitted a similar model, using the landscape-level SR of taxonomic groups standardized within each taxon and region as the response variable. To reflect that species pools vary between taxa, we added taxon as a random effect.

*Model 3: lmer (SR ∼ CD*MFS*SNC +* CD^2 *+* MFS^2 *+* SNC^2 *+ CropNb + Lat + Lon + (1|Region/Year) + (1|Taxon)).* Then we added random effects for taxon on the slopes of CD, MFS, SNC, as well as the interaction between CD and SNC (model 4). We assumed that the effects of taxon on the intercept and slopes were uncorrelated. To test whether taxon had a significant effect on the slope of either

CD, MFS, SNC or the interaction between CD and SNC, we used the function exactRLRT from package RLRsim.

Model 4: $\mathit{lmer}\ (SR \sim CD * MFS * SNC + CD^2 + MFS^2 + SNC^2 + CropNb + Lat + Lon + (1|Taxon) + (1|Region/Year) + (0{+}CD|\ Taxon)) + (0{+}MFS|Taxon) + (0{+}SNC|\ Taxon) + (0{+}CD{:}SNC|\ Taxon))$. We fitted all models with the R lme4 package using LMER (44), we removed outliers using function romr.fnc from package LMERConvenienceFunctions (45), and we ran diagnostic tools to verify that residuals were independently and normally distributed, and showed no spatial autocorrelation. For each model, a multimodel inference procedure was applied using the R MuMIn package (46). This method allowed us to perform model selection by creating a set of models with all possible combinations of the initial variables and sorting them according to the Akaike Information Criterion (AIC) fitted with Maximum Likelihood (47). We selected all models with ΔAIC <2 and used the model averaging approach using LMER to estimate parameters and associated *P* values, using the function model.avg. We ran all analyses using the software R 3.4.0 (48).

We ran additional analyses to check that the composition of the crop mosaic, the proportion of grassland in the crop mosaic, and the amount of seminatural vegetation occurring between fields did not affect our conclusions (*SI Appendix*, section 5). We also ran complementary analyses using field-level multidiversity (T60.field) as the response variable—instead of the landscape-level multidiversity index (T60.landscape)—to check that our results hold true at the field level, in particular within a subset of cereal fields, and that the type of crop sampled or the level of land-use intensity within sampled fields did not affect our conclusions (*SI Appendix*, section 5). Finally, we used a moving window analysis to identify potential discontinuities in multitrophic diversity response to CD and MFS along the gradient of SNC (*SI Appendix*, section 5).

Data Accessibility. All protocols, datasets, and R codes used in this article can be made available upon request to the corresponding author.

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