This is a previous version of the article published in Proceedings of the National Academy of Sciences. 2019, 116(33): 16442-16447. doi:10.1073/pnas.1906419116

Classification: BIOLOGICAL SCIENCES - Ecology

Title: **Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions**

Short title: **Crop heterogeneity and multitrophic diversity**

Clélia Sirami[1,2,3], Nicolas Gross[4,5,6], Aliette Bosem Baillod[7,8]*, Colette Bertrand[9,10,11]*, Romain Carrié[2,12]*, Annika Hass[7]*, Laura Henckel[5,13,14,15]*, Paul Miguet[5,13,14,16]*, Carole Vuillot[1,17]*, Audrey Alignier[9,18], Jude Girard[19], Péter Batáry[7,20], Yann Clough[7,12], Cyrille Violle[1], David Giralt[21], Gerard Bota[21], Isabelle Badenhauser[5,13,14], Gaetan Lefebvre[22], Bertrand Gauffre[5,13,14], Aude Vialatte[2,3], François Calatayud[2,3], Assu Gil-Tena[23], Lutz Tischendorf[19], Scott Mitchell[19], Kathryn Lindsay[19], Romain Georges[11], Samuel Hilaire[22], Jordi Recasens[24], Xavier Oriol Solé-Senan[24], Irene Robleño[24], Jordi Bosch[25], Jose Antonio Barrientos[26], Antonio Ricarte[27], Maria Ángeles Marcos-Garcia[27], Jesus Minano[28], Raphael Mathevet[1], Annick Gibon[2], Jacques Baudry[9,18], Gerard Balent[2], Brigitte Poulin[22], Françoise Burel[11,18], Teja Tscharntke[7], Vincent Bretagnolle[5,13,14], Gavin Siriwardena[29], Annie Ouin[2,3], Lluis Brotons[21,23,30], Jean-Louis Martin[1]**, Lenore Fahrig[19]**

*These co-authors contributed equally as part of their PhDs.
**These co-authors contributed equally to the project coordination.

Author affiliation:
[1] Centre d'Écologie Fonctionnelle et Évolutive UMR 5175, CNRS – Université de Montpellier – Université Paul Valéry Montpellier – EPHE - IRD, 1919 route de Mende, 34293 Montpellier Cedex 5, France
[2] Dynafor, Université de Toulouse, INRA, Castanet-Tolosan, France
[3] LTSER Zone Atelier « PYRÉNÉES GARONNE », 31320 Auzeville-Tolosane, France
[4] UCA, INRA, VetAgro Sup, UMR Ecosystème Prairial, 63000 Clermont-Ferrand, France
[5] LTER « Zone Atelier Plaine et Val de Sèvre » - Centre d'Etudes Biologiques de Chizé, Villiers en Bois, F-79360, France
[6] Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, C/ Tulipán s/n, 28933 Móstoles, Spain
[7] Agroecology, Department for Crop Sciences, University of Goettingen, Grisebachstr. 6 D-37077 Göttingen, Germany
[8] Agroscope, Reckenholzstrasse 191, CH-8046 Zurich, Switzerland
[9] U.M.R. 0980 BAGAP, INRA, Agrocampus Ouest, ESA. 65 Rue de Saint-Brieuc CS 84215, 35042 Rennes Cedex, France
[10] U.M.R. 1402 ECOSYS, I.N.R.A., AgroParisTech, Université Paris-Saclay. 78026 Versailles, France
[11] U.M.R. 6553 ECOBIO, CNRS, 35042 Rennes, France
[12] Centre for Environmental and Climate Research, Lund University, Sölvegatan 37, SE-22362 Lund, Sweden
[13] CNRS–Université de La Rochelle, U.M.R. 7372, Centre d'Etudes Biologiques de Chizé, Villiers en Bois, F-79360, France
[14] INRA, USC1339, Station d'Ecologie de Chizé-La Rochelle, Villiers en Bois, F-79360, Niort, France
[15] Swedish Species Information Centre, Swedish University of Agricultural Sciences (SLU), Box 7007, SE-75007 Uppsala, Sweden

[16] INRA, UR1115 Plantes et Systèmes de Culture Horticoles, Domaine Saint Paul, Site Agroparc, 84914 Avignon Cedex 9, France
[17] Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR 7204), Sorbonne Universités, CNRS, UPMC, Muséum National d'Histoire Naturelle, CP 51, 55 Rue Buffon, 75005 Paris – France
[18] LTER « Zone Atelier Armorique » - U.M.R. 0980 BAGAP, 35042 Rennes Cedex, France
[19] Geomatics and Landscape Ecology Laboratory, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, Canada K1S 5B6
[20] MTA ÖK Landscape and Conservation Ecology Research Group, Alkotmány u. 2-4, 2163 Vácrátót, Hungary
[21] CTFC Forest Sciences Centre of Catalonia, 25280 Solsona, Catalonia, Spain
[22] Tour du Valat Research Institute for the conservation of Mediterranean wetlands, Le Sambuc, 13200 Arles, France
[23] InForest Joint Research Unit (CTFC-CREAF), 25280 Solsona, Spain
[24] Agrotecnio. ETSEA, Dept HBJ, Universitat de Lleida. Alcalde Rovira Roure 191, 25198, Lleida, Spain
[25] CREAF, 08193 Cerdanyola del Vallès, Spain
[26] Universitat Autònoma Barcelona, 08193 Cerdanyola Del Vallès, Spain
[27] Instituto Universitario de Investigacio´n, CIBIO, Centro Iberoamericano de la Biodiversidad, University of Alicante, 03690 San Vicente del Raspeig, Alicante, Spain
[28] Facultad de Biología, Universidad de Murcia, 30100 - Campus de Espinardo, Murcia, Spain
[29] British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK
[30] CSIC, 08193 Cerdanyola del Vallès, Spain

Corresponding author:
Clélia Sirami U.M.R. 1201 Dynafor, I.N.R.A. – I.N.P. Toulouse - E.N.S.A.T., Chemin de Borde Rouge BP 52627, 31326 Castanet Tolosan Cedex, France. Tel: 0033561285351. Email: clelia.sirami@inra.fr

Keywords: multi-taxa, agricultural landscapes, crop mosaic, farmland, landscape complementation

ABSTRACT

Agricultural landscape homogenization has detrimental effects on biodiversity and key ecosystem services. Increasing agricultural landscape heterogeneity by increasing semi-natural cover can help to mitigate biodiversity loss. However, the amount of semi-natural 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 eight 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 three sampling sites in one, two or three crop types. We sampled seven taxa (plants, bees, butterflies, hoverflies, carabids, spiders, birds) and calculated a synthetic index of multitrophic diversity at the landscape level. Increasing crop heterogeneity was more beneficial for multitrophic diversity than increasing semi-natural cover. For instance, the effect of decreasing mean field size from 5 to 2.8 ha was as strong as the effect of increasing semi-natural cover from 0.5 to 11 %. Decreasing mean field size benefited multitrophic diversity even in the absence of semi-natural 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 semi-natural cover. Our study provides the first 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.

SIGNIFICANCE STATEMENT

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 semi-natural 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 semi-natural cover in the landscape, across 435 agricultural landscapes located in eight 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.

INTRODUCTION

Agriculture dominates the world's terrestrial area (1, 2). Agricultural landscape homogenization through the decrease of semi-natural cover, crop specialization and field enlargement (3–6) represents a continuing worldwide threat to biodiversity and the delivery of key ecosystem services to people (7, 8). There is ample evidence that enhancing landscape heterogeneity by reversing the decline in semi-natural cover can benefit biodiversity in agricultural landscapes (9–12). However, the amount of semi-natural cover keeps decreasing in many agricultural landscapes, and the efficiency of policies focusing solely on maintaining or increasing semi-natural cover has been questioned (13).

While half of the biodiversity in agricultural landscapes occurs exclusively in semi-natural cover (14), 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 (15–17). 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 re-arrangement 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, 18; see further explanation in *Methods*). These two components of crop heterogeneity may influence farmland biodiversity in several ways (see detailed alternative hypotheses in SI 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 1; 19). 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 1; 20). 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 1; 20, 21). 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 non-linear and non-additive. 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 semi-natural cover in the landscape. For instance, the 'intermediate landscape-complexity' hypothesis (22) predicts that the positive biodiversity-crop heterogeneity relationship is stronger in landscapes with intermediate amounts of semi-natural habitats (e.g. 5-20%) than in landscapes with little (e.g. <5%) or much semi-natural habitat (e.g. >20%; 10). Sampling over a wide range of landscapes may therefore be necessary to understand the general effect of crop heterogeneity on farmland biodiversity.

The biodiversity-crop heterogeneity relationship may vary among taxa (e.g. 23, 24). For instance, it may be more positive for species and taxa that have lower habitat area requirements (e.g. small species; 25) or higher habitat specialization levels (e.g. 26). 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 (27, 28). 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 in order to identify landscape patterns that simultaneously increase the diversity of most taxa (29).

We selected 435 landscapes along orthogonal gradients of mean size and diversity of crop types available in the landscape in eight contrasting agricultural regions in France, the United Kingdom, Germany, Spain and Canada (Fig. S2.1 in SI 2). In each landscape, we selected three sampling sites in one, two or three crop types. We sampled seven 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 semi-natural 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 non-linear, non-additive, and influenced by semi-natural cover (see detailed hypotheses in SI 1).

RESULTS AND DISCUSSION

Our study provides the first 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, the mean size and diversity of crop types available in the landscape were consistently included in all models (Fig. 2A). Together, they accounted for 61% of the explained variance in multitrophic diversity, while semi-natural cover accounted for 24% (Fig. 2B). Interactions between semi-natural 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 is modulated by the amount of semi-natural cover in the landscape (Fig. 3). The effects of crop heterogeneity on multitrophic diversity were consistent across the eight 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 seven taxa (Fig. 5 and Fig. S5.2 in SI 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 eight regions (Table S5.11 in SI 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 ploughing, 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 (see additional analyses in SI 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 size² together accounting for 47.4% of the explained variance in multitrophic diversity (Fig. 2B). The effect of decreasing mean field size from 5 to 2.75 ha was as strong as the effect of increasing semi-natural cover from 0.5 to 11 % of the landscape (Fig. 3B). 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; 20, 21). 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 section 5.3 in SI 5). It was also consistently positive across all group of taxa considered separately, from primary producers to predators (Fig. 5 and section 5.4 in SI 5). Previous studies have already reported positive effects of decreasing mean field size on the diversity of several taxa considered separately (30–34). 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 semi-natural vegetation between fields (30–34). To test this hypothesis, we selected a subset of landscapes for which mean field size and the length of semi-natural vegetation between fields were uncorrelated (see details in section 5.5.3 in SI 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 semi-natural vegetation between fields. Increasing the amount of semi-natural 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 in SI 5). This result suggests that smaller fields benefit multitrophic diversity even in the absence of semi-natural vegetation between fields.

Finally, the presence of the interaction term between mean field size and semi-natural cover in our model (Fig. 2A) suggests that the effect of mean field size on multitrophic diversity tends to be modulated by the amount of semi-natural cover available in the landscape (Fig. 3B). To further explore this interaction, we used a moving window modeling approach (35; see details in section 5.7 in SI 5). This analysis confirmed that decreasing mean field size had a consistent positive effect on multitrophic diversity along the gradient of semi-natural cover. Moreover, it suggested that this effect is stronger when semi-natural cover is below 8%, i.e. when semi-natural cover is too scarce to provide access to the multiple resources required by most species occurring in agricultural landscapes (Fig. S5.5.B in SI 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. 2A). 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 (see further explanations in SI 1 and section 4.4. in SI 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. 2B). 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 1, 26).

The main effect of increasing the diversity of crop types available in the landscape was non-significant but the effect was significantly mediated by semi-natural cover. These effects were consistent across all regions (Fig. 4). Together, the diversity of crop types available in the landscape and its interaction with semi-natural cover accounted for 10% of the explained variance in multitrophic diversity (Fig. 2B). The landscape-level effect of increasing crop diversity on multitrophic diversity ranged from negative in landscapes with low semi-natural cover to positive in landscapes with high semi-natural cover (Fig. 3A). This result is consistent with the variability of effects observed across previous studies (30, 32, 34, 36, 37). To further explore this interaction, we used the same moving window modeling approach described above (see section 5.7 in SI 5 for details). This analysis confirmed that the landscape-level effect of increasing crop diversity on multitrophic diversity was positive in landscapes with more than 11% semi-natural cover (i.e. 50% of landscapes included in our study), non-significant in landscapes with 4 to 11% semi-natural cover (i.e. 34% of landscapes), and negative in landscapes with less than 4% semi-natural cover (i.e. 16% of landscapes; Fig. S5.5.A in SI 5).

The positive landscape-level effect of increasing crop diversity on multitrophic diversity observed in landscapes with more than 11% semi-natural cover supports the 'landscape complementation' hypothesis (Hyp 1b in SI 1). This finding is consistent with the fact that a diverse crop matrix provides a temporal continuity of food sources (38) while semi-natural patches provide stable resources, for example, for nesting or shelter (e.g. 37). Such complementation among multiple cover types has been described for several species (e.g. 38–40). 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% semi-natural cover supports the 'minimum total habitat area requirement' hypothesis (Hyp 1c in SI 1). This finding is consistent with the fact that landscape simplification tends to filter out species with large body sizes (43), which also have high minimum total habitat area requirements (44), and may therefore require high amount of a single crop type. However, the whole range of taxa included in the present study, associated with a wide range of ecological traits, and therefore a wide range of minimum total habitat area requirements, showed a consistent response to crop diversity and the interaction of crop diversity and semi-natural cover (Fig. 5). The 'minimum total habitat area requirement' hypothesis therefore seems unlikely to solely explain our results. Other hypotheses developed in the literature include the role of crop identity and management practices (e.g. 41). We considered the possibility that, at low levels of semi-natural cover, landscapes with higher crop diversity may have more intensive management practices, thus reducing multitrophic diversity (as suggested in 34). For example, in Armorique and PVDS, the increase in crop diversity was associated with a decrease in the cover of clover, a crop type associated with extensive management practices, and an increase in the cover of potatoes, a crop type associated with very intensive management practices (45). Reasons for the negative landscape-level effect of increasing crop diversity on multitrophic diversity in landscapes with low semi-natural cover deserve further attention. Future research is needed to identify conditions under which increasing crop diversity leads to a consistent net positive effect on multitrophic diversity, i.e. a positive effect of field-level (i.e. habitat specialization) plus landscape-level (i.e. 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 (27), the Canadian Agriculture Policy Frameworks (46), or the United States Farm Bill (47).

First, our results suggest that increasing crop heterogeneity may have a similar or greater benefit for multitrophic diversity to increasing semi-natural cover (Fig. 2B) or even decreasing field-level land use intensity (21; Table S5.12 in SI 5). Given current challenges to increase semi-natural cover and limit chemical use in agricultural landscapes (48), 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 semi-natural cover or reduce chemical use (49). 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 (48). Such measures may also contribute to the development of new frameworks that reward farmers for sustainable land stewardship (50).

We observed a consistent effect of crop heterogeneity on species diversity across seven 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 six or even all seven 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 semi-natural 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 semi-natural cover exceeds 11%. However, they may have little effect or may even have negative effects in intensive agricultural landscapes with little semi-natural cover. Our study therefore highlights that measures promoting an increase in crop diversity are more likely to be effective in promoting multitrophic diversity across all agricultural landscapes if combined with measures promoting the restoration or maintenance of semi-natural 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 semi-natural 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.

METHODS

1. Region, landscape and sampling site selection

We selected eight 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 in SI 2) belonging to six different ecoregions (51) 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 prior to 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 compositional heterogeneity (crop diversity) and crop configurational heterogeneity (mean field size) while minimizing the correlation between them (52). 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 x 1 km landscapes. We selected between 32 and 93 landscapes within each region, totaling 435 landscapes across all regions.

We selected three sampling sites within each landscape, totaling 1305 sampling sites across all regions. The number of crop types sampled ranged from one to three 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 3). The three 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 non-agricultural cover types such as forests and urban areas.

2. Multi-taxa sampling

We selected seven 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 eight regions (Section 3.1 in SI 3).

At each sampling site, we selected two parallel 50 m ‘transects’, one located at the field edge and the other inside the field 25 m away from the first transect (Fig. S3.1 and S3.2 in SI 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 priori to identification. Multiple survey visits were conducted during the season when relevant (SI 3). Each landscape was sampled during one year and sampling of landscapes was distributed across two years within each region, between 2011 and 2014 (see further details on the timing of our sampling in Table S3.1 in SI 3).

We identified more than 167,000 individuals from 2795 species (Table S3.2 in SI 3). For each taxon, we calculated species richness at the landscape level, i.e. across all three 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 in SI 3).

3. Multitrophic diversity index

Our objective was to identify landscapes where the diversity of most taxa increases simultaneously. A first approach used in the literature consists of calculating the average, standardized diversity across taxa (53). However, this approach has limitations (see section 3.3 in SI 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 (i) diversity values are intermediate for all taxa, or (ii) 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 (29, 54). For each taxon and each region, we identified the maximum species richness observed across all landscapes. We actually used the 95^{th} percentile as the maximum observed species richness (hereafter ‘SR max’) in order to minimize the effect of outliers. Next, we identified which landscapes attained a given threshold (x) of SR max. We then tallied the proportion of taxa that exceeded the given threshold in order to produce a multidiversity index (Tx.landscape) for each landscape, based on the following formula:

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

where n is the number of taxa for which data were available in a given landscape (see details in section 3.2 in SI 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 belonged to. This multidiversity index ranges between 0 and 1.

We calculated this multidiversity index for each threshold x between 20 and 90% (every 10%). For each threshold x, the multidiversity index was smoothed by calculating the average over the interval [x − 10%, x + 10%] (55; see details in section 3.3 in SI 3). Multidiversity indices calculated for different thresholds were strongly correlated. We chose to use the intermediate threshold T60.landscape because 1) intermediate thresholds have been shown to provide an effective measure of multitrophic diversity in agricultural landscapes (53) and 2) T60.landscape shows a distribution ranging from 0, i.e. none of the taxa reach 60% of the regional maximum, to 100, i.e. all taxa reach 60% of the regional maximum (mean value for T60.landscape = 45.1). Nevertheless, we verified that our results were not sensitive to the threshold selected (Fig. S5.2 in SI 5). For simplicity, we hereafter refer to "landscape-level multitrophic diversity" rather than T60.landscape.

4. Crop compositional and configurational heterogeneity

We used a standardized protocol across all regions to produce land cover maps allowing us to compare consistency of effects across the eight regions (SI 4). We conducted extensive ground-truthing surveys during the field seasons to map all fields, linear elements between adjacent fields, and non-agricultural covers. We built a common land cover classification for the eight regions. Agricultural cover types included all crops, as well as temporary and permanent grassland managed for production purposes (SI 4). Linear elements between fields included hedgerows, grassy margins, ditches and tracks. Non-agricultural cover types included woodland (including woody linear elements), open land (e.g. extensive grassland, shrubland, grassy linear elements), wetland and built-up areas (including roads). We then used these standardized, detailed maps to calculate four explanatory variables for each landscape: crop diversity, mean field size, semi-natural cover and total length of semi-natural linear elements between fields.

We used the Shannon diversity of agricultural cover types (hereafter "crop diversity"; CD) as a measure of crop compositional heterogeneity. We used mean field size in hectares (MFS) as a measure of crop configurational heterogeneity. Neither CD nor MFS was correlated with local land use intensity (an index combining data on ploughing, fertilizer, herbicide and insecticide, see section 5.6.3 in SI 5) or the overall composition of the crop mosaic (section 5.5.1 in SI 5) across all regions. 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 (sections 5.5.1 and 5.5.2 in SI 5). We calculated the percentage of semi-natural cover types, i.e. woodland, open land and wetland (SNC), in each landscape. We also calculated the total length of linear semi-natural elements between fields, e.g. hedgerows, grassy margins (SNL; measured in meters). SNL and MFS were highly correlated in some regions (Table S5.6 in SI 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 (section 5.5.3 in SI 5).

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), crop diversity (CD), mean field size (MFS) and semi-natural cover (SNC) as explanatory variables (see alternative hypotheses on crop heterogeneity-biodiversity relationships in SI 1). We included both interaction effects and quadratic effects. Due to a positive skew in the distribution of mean field size, we used log mean field size 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))

To test whether the effects of crop diversity, mean field size and semi-natural cover on multitrophic diversity measured at the landscape level (T60.landscape) varied significantly among regions we added random effects for region on the slopes of crop diversity, mean field size, semi-natural cover as well as the interaction between crop diversity and semi-natural cover (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 crop diversity, mean field size, semi-natural cover as well as the interaction between crop diversity and semi-natural cover, 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 species richness of taxonomic groups (Model 3). To do this, we fitted a similar model, using the landscape-level species richness of taxonomic groups (SR) 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 + CD² + MFS² + SNC² + CropNb + Lat + Lon + (1|Region/Year) + (1|Taxon))*

To test whether the effects of crop diversity, mean field size and semi-natural cover on the species richness of taxonomic groups varied significantly among taxa we added random effects for Taxon on the slopes of crop diversity, mean field size, semi-natural cover as well as the interaction between crop diversity and semi-natural cover (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 crop diversity, mean field size, semi-natural cover or the interaction between crop diversity and semi-natural cover, we used the function exactRLRT from package RLRsim.

*Model 4: lmer (SR ~ CD * MFS * SNC + CD² + MFS² + SNC² + 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 (56), we removed outliers using function romr.fnc from package LMERConvenienceFunctions (57) 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 (58). 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 (59). 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 (60).

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 semi-natural vegetation occurring between fields did not affect our conclusions (section 5.5 in SI 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 (section 5.6 in SI 5). Finally, we used a moving window analysis to identify potential discontinuities in multitrophic diversity response to crop diversity and mean field size along the gradient of semi-natural cover (section 5.7 in SI 5).

Acknowledgments

This research was funded by the ERA-Net BiodivERsA, with the national funders French National Research Agency (ANR-11-EBID-0004), German Ministry of Research and Education, German Research Foundation and Spanish Ministry of Economy and Competitiveness, part of the 2011 BiodivERsA call for research proposals. The UK component of this research was funded by the UK Government Department of the Environment, Food and Rural Affairs (Defra), as project WC1034. The Canadian component of this research was funded by a Natural Sciences and Engineering Research Council of Canada (NSERC) Strategic Project, the Canada Foundation for Innovation, Environment Canada (EC), and Agriculture and Agri-Food Canada (AAFC). N.G. was support by the AgreenSkills+ fellowship programme which has received funding from the EU's Seventh Framework Programme under grant agreement N° FP7-609398 (AgreenSkills+ contract). A. G.-T. (Juan de la Cierva fellow, JCI-2012-12089) was funded by Ministerio de Economía y Competitividad (Spain). C. Violle was supported by the European Research Council (ERC) Starting Grant Project "Ecophysiological and biophysical constraints on domestication of crop plants" (Grant ERC-StG-2014-639706-CONSTRAINTS). A.R.'s position at the University of Alicante is funded by the 'Vicerrectorado de Investigación y Transferencia de Conocimiento'. We would like to thank the hundreds of farmers and farm owners from all eight regions who graciously permitted us to work on their lands. In addition to the co-authors, the project involved direct assistance from more than 150 individuals for geomatics analyses, field sampling, and species identification. We would like to thank all of them for their huge contribution to the FarmLand project and this study. Finally, we are grateful to the GLEL Friday Discussion Group for very helpful input.

Author contribution

CS and NG wrote the first draft of the manuscript; BP, FB, TT, VB, GS, AO, LB, JLM and LF designed the FarmLand project; CS, ABB, CB, RC, AH, LH, PM, AA, JG, DG, G Bota, FC, AGT, RG, SH, JR, XOSS, IR, JB, JAB, AR, MAM-G, JM and GS contributed data; CS, NG, ABB, CB, RC, AH, LH, PM and AA analyzed data; all co-authors provided feedback on the manuscript.

References

1. Tilman D, et al. (2001) Forecasting agriculturally driven global environmental change. *Science* 292(5515):281–284.

2. Foley JA, et al. (2005) Global consequences of land use. *Science* 309(5734):570–574.

3. Robinson RA, Sutherland WJ (2002) Post-war changes in arable farming and biodiversity in Great Britain. *J Appl Ecol* 39(1):157–176.

4. White EV, Roy DP (2015) A contemporary decennial examination of changing agricultural field sizes using Landsat time series data. *Geo Geogr Environ* 2(1):33–54.

5. Barr CJ, Gillespie MK (2000) Estimating hedgerow length and pattern characteristics in Great Britain using Countryside Survey data. *J Environ Manage* 60(1):23–32.

6. Aguilar J, et al. (2015) Crop Species Diversity Changes in the United States: 1978–2012. *PLoS ONE* 10(8). doi:10.1371/journal.pone.0136580.

7. Newbold T, et al. (2015) Global effects of land use on local terrestrial biodiversity. *Nature* 520(7545):45–50.

8. Maxwell SL, Fuller RA, Brooks TM, Watson JEM (2016) Biodiversity: The ravages of guns, nets and bulldozers. *Nature* 536(7615):143–145.

9. Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol Evol* 18(4):182–188.

10. Batáry P, Fischer J, Báldi A, Crist TO, Tscharntke T (2011) Does habitat heterogeneity increase farmland biodiversity? *Front Ecol Environ* 9(3):152–153.

11. Miyashita T, Chishiki Y, Takagi SR (2012) Landscape heterogeneity at multiple spatial scales enhances spider species richness in an agricultural landscape. *Popul Ecol* 54(4):573–581.

12. Perović D, et al. (2015) Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. *J Appl Ecol* 52(2):505–513.

13. Batáry P, Dicks LV, Kleijn D, Sutherland WJ (2015) The role of agri-environment schemes in conservation and environmental management. *Conserv Biol* 29(4):1006–1016.

14. Lüscher G, et al. (2016) Farmland biodiversity and agricultural management on 237 farms in 13 European and two African regions. *Ecology* 97(6):1625–1625.

15. Henderson IG, Vickery JA, Carter N (2004) The use of winter bird crops by farmland birds in lowland England. *Biol Conserv* 118(1):21–32.

16. Holzschuh A, Dormann CF, Tscharntke T, Steffan-Dewenter I (2013) Mass-flowering crops enhance wild bee abundance. *Oecologia* 172(2):477–484.

17. Raymond L, et al. (2014) Immature hoverflies overwinter in cultivated fields and may significantly control aphid populations in autumn. *Agric Ecosyst Environ* 185:99–105.

18. Fahrig L, et al. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol Lett* 14(2):101–112.

19. Weibull A-C, Östman Ö, Granqvist Å (2003) Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodivers Conserv* 12(7):1335–1355.

20. Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. *Oikos* 65(1):169–175.

21. Batáry P, et al. (2017) The former Iron Curtain still drives biodiversity-profit trade-offs in German agriculture. *Nat Ecol Evol* 1(9):1279–1284.

22. Tscharntke T, et al. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol Rev* 87(3):661–685.

23. Burel F, Butet A, Delettre YR, de la Pena NM (2004) Differential response of selected taxa to landscape context and agricultural intensification. *Landsc Urban Plan* 67(1–4):195–204.

24. Dormann CF, et al. (2007) Effects of landscape structure and land-use intensity on similarity of plant and animal communities. *Glob Ecol Biogeogr* 16(6):774–787.

25. Ponjoan A, Bota G, Mañosa S (2012) Ranging behaviour of little bustard males, Tetrax tetrax, in the lekking grounds. *Behav Processes* 91(1):35–40.

26. Gaba S, Chauvel B, Dessaint F, Bretagnolle V, Petit S (2010) Weed species richness in winter wheat increases with landscape heterogeneity. *Agric Ecosyst Environ* 138(3–4):318–323.

27. Pe'er G, et al. (2014) EU agricultural reform fails on biodiversity. *Science* 344(6188):1090–1092.

28. Díaz S, et al. (2015) The IPBES Conceptual Framework — connecting nature and people. *Curr Opin Environ Sustain* 14:1–16.

29. Allan E, et al. (2014) Interannual variation in land-use intensity enhances grassland multidiversity. *Proc Natl Acad Sci U S A* 111(1):308–313.

30. Fahrig L, et al. (2015) Farmlands with smaller crop fields have higher within-field biodiversity. *Agric Ecosyst Environ* 200:219–234.

31. Collins SJ, Fahrig L (2017) Responses of anurans to composition and configuration of agricultural landscapes. *Agric Ecosyst Environ* 239(Supplement C):399–409.

32. Monck-Whipp L, Martin AE, Francis CM, Fahrig L (2018) Farmland heterogeneity benefits bats in agricultural landscapes. *Agric Ecosyst Environ* 253(Supplement C):131–139.

33. Šálek M, et al. (2018) Bringing diversity back to agriculture: Smaller fields and non-crop elements enhance biodiversity in intensively managed arable farmlands. *Ecol Indic* 90:65–73.

34. Hass AL, et al. (2018) Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. *Proc R Soc B* 285(1872):20172242.

35. Berdugo M, et al. Aridity preferences alter the relative importance of abiotic and biotic drivers on plant species abundance in global drylands. *J Ecol* 0(0). doi:10.1111/1365-2745.13006.

36. Josefsson J, Berg Å, Hiron M, Pärt T, Eggers S (2017) Sensitivity of the farmland bird community to crop diversification in Sweden: does the CAP fit? *J Appl Ecol* 54(2):518–526.

37. Olimpi EM, Philpott SM (2018) Agroecological farming practices promote bats. *Agric Ecosyst Environ* 265:282–291.

38. Schellhorn NA, Gagic V, Bommarco R (2015) Time will tell: resource continuity bolsters ecosystem services. *Trends Ecol Evol* 30(9):524–530.

39. Sirami C, Brotons L, Martin J (2011) Woodlarks Lullula arborea and landscape heterogeneity created by land abandonment. *Bird Study* 58(1):99–106.

40. Pope SE, Fahrig L, Merriam NG (2000) Landscape complementation and metapopulation effects on leopard frog populations. *Ecology* 81(9):2498–2508.

41. Mueller T, Selva N, Pugacewicz E, Prins E (2009) Scale-sensitive landscape complementation determines habitat suitability for a territorial generalist. *Ecography* 32(2):345–353.

42. Marrec R, et al. (2015) Crop succession and habitat preferences drive the distribution and abundance of carabid beetles in an agricultural landscape. *Agric Ecosyst Environ* 199:282–289.

43. Gámez-Virués S, et al. (2015) Landscape simplification filters species traits and drives biotic homogenization. *Nat Commun* 6:8568.

44. Baguette M, Stevens V (2013) Predicting minimum area requirements of butterflies using life-history traits. *J Insect Conserv* 17(4):645–652.

45. Agreste (2013) Les indicateurs de fréquence de traitement (IFT) en 2011. *Doss* 18.

46. Deaton BJ, Boxall P (2017) Canadian Agricultural Policy in the Twenty-First Century: Looking Back and Going Forward. *Can J Agric Econ Can Daposagroeconomie* 65(4):519–522.

47. Reimer A (2015) Ecological modernization in U.S. agri-environmental programs: Trends in the 2014 Farm Bill. *Land Use Policy* 47(Supplement C):209–217.

48. Pe'er G, et al. (2017) Adding Some Green to the Greening: Improving the EU's Ecological Focus Areas for Biodiversity and Farmers. *Conserv Lett* 10(5):517–530.

49. Rodríguez C, Wiegand K (2009) Evaluating the trade-off between machinery efficiency and loss of biodiversity-friendly habitats in arable landscapes: The role of field size. *Agric Ecosyst Environ* 129(4):361–366.

50. Mathevet R, Bousquet F, Raymond CM (2018) The concept of stewardship in sustainability science and conservation biology. *Biol Conserv* 217:363–370.

51. Olson DM, et al. (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* 51(11):933–938.

52. Pasher J, et al. (2013) Optimizing landscape selection for estimating relative effects of landscape variables on ecological responses. *Landsc Ecol* 28(3):371–383.

53. Byrnes JEK, et al. (2014) Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. *Methods Ecol Evol* 5(2):111–124.

54. Zavaleta ES, Pasari JR, Hulvey KB, Tilman GD (2010) Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proc Natl Acad Sci U S A* 107(4):1443–1446.

55. Le Bagousse-Pinguet Y, et al. (2019) Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality. *Proc Natl Acad Sci*:201815727.

56. Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67(1):1–48.

57. Tremblay A, Ransijn J (2015) *LMERConvenienceFunctions: Model Selection and Post-hoc Analysis for (G)LMER Models*.

58. Barton K (2009) MuMIn : multi-model inference, R package version 0.12.0. *Httpr-Forg-Proj*. Available at: https://ci.nii.ac.jp/naid/10030574914/ [Accessed August 1, 2018].

59. Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R* (Springer New York) Available at: http://www.springer.com/in/book/9780387874579 [Accessed June 24, 2017].

60. R Core Team (2016) *R: A language and environment for statistical computing* (R Foundation for Statistical Computing. ISBN 3-900051-07-0, URL http://www.R-project.org., Vienna, Austria).

61. Grace JB, Bollen KA (2005) Interpreting the Results from Multiple Regression and Structural Equation Models. *Bull Ecol Soc Am* 86(4):283–295.

Figure legends

Figure 1. A) Traditional representations of agricultural landscapes have focused on the amount of semi-natural covers and semi-natural vegetation between fields, often considering the farmed part of the landscape as a homogeneous matrix. These representations are associated with the hypothesis that increasing the amount of semi-natural covers and semi-natural vegetation between fields benefits biodiversity. B) Novel representations of agricultural landscapes consider the heterogeneity of the crop mosaic. These representations are associated with new hypotheses: increasing crop heterogeneity by increasing crop diversity and/or decreasing mean field size, while maintaining semi-natural cover and semi-natural vegetation between fields constant, benefits biodiversity (large squares represent landscapes; adapted from 18).

Figure 2. Response of multitrophic diversity to the diversity of crop types available within the landscape (CD), the number of crops sampled (Crop Nb), mean field size (MFS), semi-natural cover (SNC), and interaction terms (CD:SNC, MFS:SNC, see further details in *Methods*), based on data collected in 435 landscapes located in eight agricultural regions. Covariates (Lon, Lat) were excluded from the figure for simplicity. A) Importance of each variable in the model averaging approach (model 1), estimated as the proportion of submodels where the variable was selected (see details in SI 5). B) The relative effect of each variable corresponds to the ratio between its parameter estimate and the sum of all parameter estimates (i.e. the % of variance explained, as explained in 60). Parameter estimates and confidence intervals, based on a model averaging approach applied to model 1 (*Methods*). ° $p<0.1$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$. Variables are grouped in three components: orange = crop heterogeneity (MFS, MFS^2, CD, CD^2, MFS:CD, Crop Nb), green = semi-natural cover (SNC, SNC^2), blue = interactive effects between crop heterogeneity and semi-natural cover (CD:SNC, MFS:SNC, CD:MFS:SNC). The % of variance explained by CD is too small to be visible.

Figure 3. Effect of the diversity of crop types available within the landscape (CD), mean field size (MFS), semi-natural cover (SNC), and their interaction terms on landscape-level multitrophic diversity (see further details in *Methods*), based on data collected in 435 landscapes located in eight agricultural regions. A) Interactive effects of crop diversity and semi-natural cover on multitrophic diversity. B) Interactive effects of mean field size and semi-natural cover on multitrophic diversity. The direction of the mean field size axis is reversed to improve readability. The parameter estimates of all other variables were fixed to their mean values, i.e. zero, as all predictors were scaled. Black dots and surfaces correspond to values of multitrophic diversity predicted by the model averaging approach applied to model 1 (*Methods*). The color gradient corresponds to multitrophic diversity values, ranging from low values (blue) to high values (red). Grey dots show the overall gradients of crop diversity, mean field size and semi-natural cover across the 435 landscapes located in eight regions.

Figure 4. Effects of the diversity of crop types available in the landscape (CD), mean field size (MFS), semi-natural cover (SNC) and the interaction between crop diversity and semi-natural cover (CD:SNC) on multitrophic diversity in different regions (see further details in *Methods*). Slopes are based on the outputs of model 2 including a random effect of region on these four slopes (n=435 landscapes). Colors indicate the region.

Figure 5. Effects of the diversity of crop types available in the landscape (CD), mean field size (log MFS), semi-natural cover (SNC) and the interaction between the diversity of crop types available in the landscape and semi-natural cover (CD:SNC) on the landscape-level species richness of taxonomic groups (see further details in *Methods*). Slopes are based on the outputs of model 10 including a random effect of taxon on these four slopes (n=435 landscapes). Colors indicate the taxon.

Figure 1.

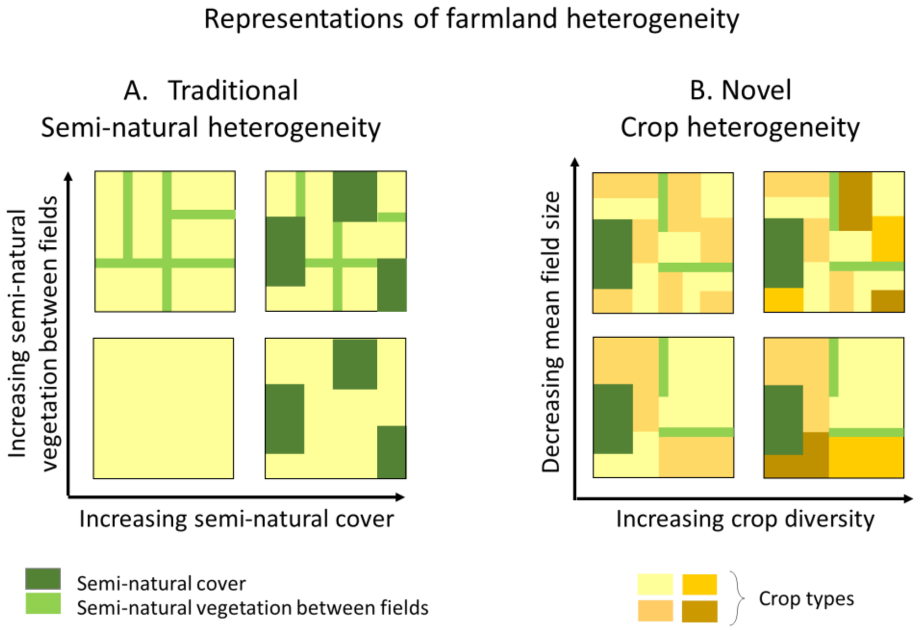
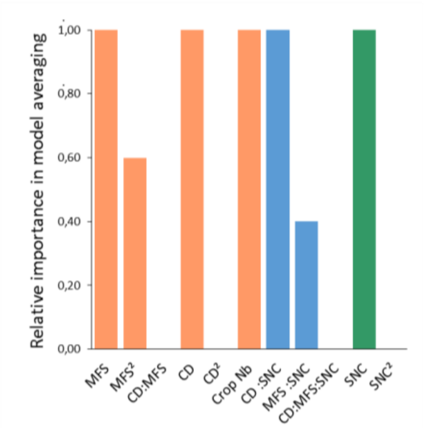

Representations of farmland heterogeneity
A. Traditional
Semi-natural heterogeneity
Increasing semi-natural vegetation between fields
Increasing semi-natural cover
Semi-natural cover
Semi-natural vegetation between fields
B. Novel
Crop heterogeneity
Decreasing mean field size
Increasing crop diversity
Crop types

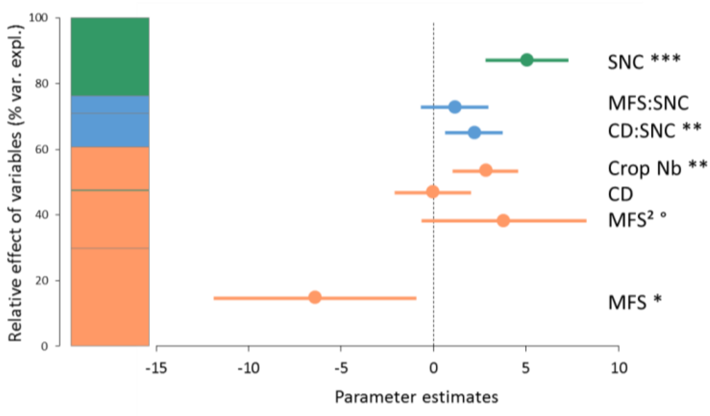
Figure 2

A



Relative importance in model averaging
1,00
0,80
0,60
0,40
0,20
0,00
MFS
MFS²
CD:MFS
CD
CD²
Crop Nb
CD :SNC
MFS :SNC
CD:MFS:SNC
SNC
SNC²

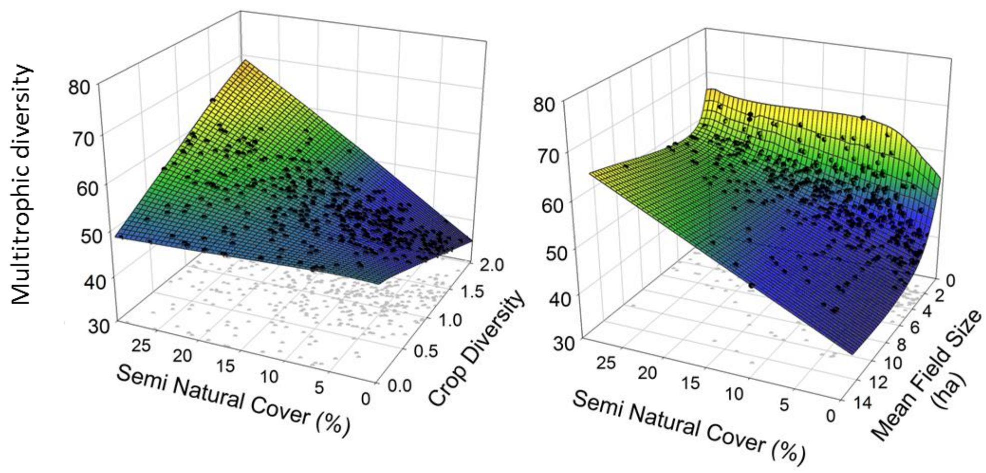
B



Relative effect of variables (% var. expl.)
100
80
60
40
20
0
SNC ***
MFS:SNC
CD:SNC **
Crop Nb **
CD
MFS² °
MFS *
-15
-10
-5
0
5
10
Parameter estimates

Figure 3.

A B



Multitrophic diversity
80
70
60
50
40
30
25
20
15
10
5
0
Semi Natural Cover (%)
0.0
0.5
1.0
1.5
2.0
Crop Diversity
Mean Field Size (ha)
0
2
4
6
8
10
12
14

Figure 4.

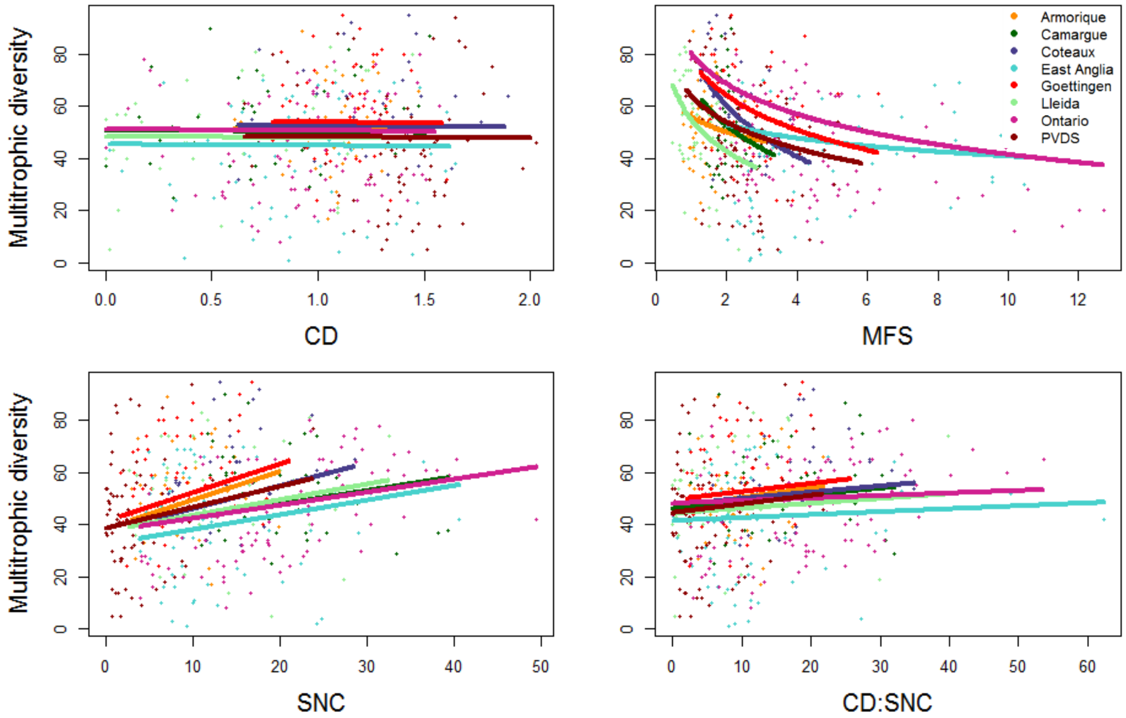
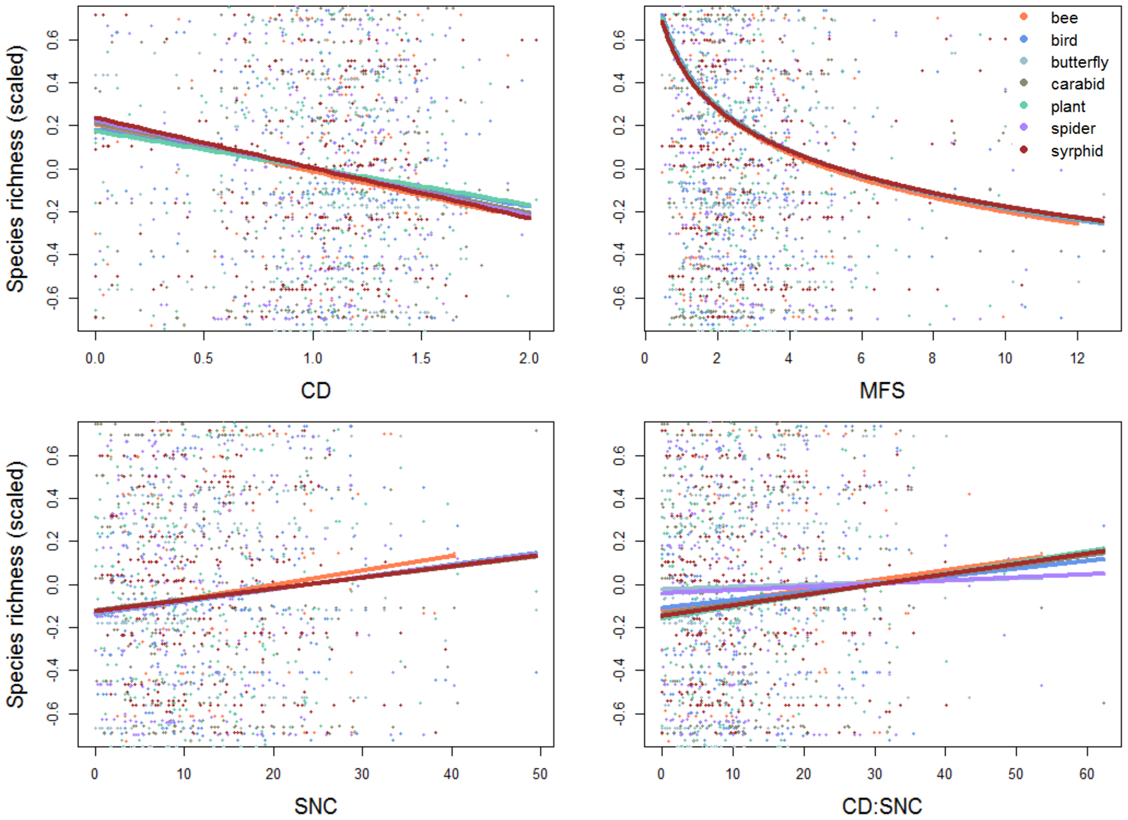

Multitrophic diversity
CD
MFS
SNC
CD:SNC
Armorique
Camargue
Coteaux
East Anglia
Goettingen
Lleida
Ontario
PVDS

Figure 5.


Species richness (scaled)
CD
MFS
SNC
CD:SNC
bee
bird
butterfly
carabid
plant
spider
syrphid
0.0
0.5
1.0
1.5
2.0
0
2
4
6
8
10
12
10
20
30
40
50
60
-0.6
-0.4
-0.2
0.2
0.4
0.6

Supporting Information

SI 1 – Hypotheses on the effects of crop heterogeneity on biodiversity
SI 2 – Region and landscape selection
SI 3 – Multitrophic diversity sampling
SI 4 – Land cover mapping and landscape metrics
SI 5 – Complementary analyses

SI 1 – Hypotheses on the effects of crop heterogeneity on biodiversity

1.1. Crop compositional heterogeneity (increasing crop diversity)

Hyp 1a. Biodiversity **increases** with increasing crop diversity if different crop types can serve as habitat for different specialized species (single habitat specialization; Andreasen et al. 1991; Weibull et al. 2003). In that case, sampling more crop types will result in observing higher landscape-level biodiversity.

Hyp 1b. Biodiversity **increases** with increasing crop diversity if different crop types provide different resources required for single species (landscape complementation; Dunning et al. 1992), or if specialist species spillover from other crop types in the landscape into the fields sampled (Duelli 1997, Schneider et al. 2016). In that case, for a given number of crop types sampled, landscapes with higher crop diversity will result in observing higher landscape-level biodiversity.

Hyp 1c. Biodiversity **decreases** with crop diversity if most species have high minimum total habitat area requirements, i.e. require large amounts of a single crop type. An increase in the number of crop types available in the landscape results in a decrease in the total area of each crop type available in the landscape, which could hypothetically result in insufficient resources for species associated with individual crop types (Fahrig et al. 2011; Tscharntke et al. 2012).

Hyp 1d. Biodiversity shows a **peaked relationship** with crop diversity available in the landscape (Allouche et al. 2012) if there is an initial increase in biodiversity with increasing crop diversity for reasons explained in Hyp 1a-1b, but at higher levels of crop diversity, each crop type has a lower spatial cover and biodiversity decreases for reasons explained in Hyp 1c.

1.2. Crop configurational heterogeneity (decreasing mean field size)

Hyp 2a. Biodiversity **increases** with decreasing mean field size if landscapes with smaller fields provide easier access to multiple fields for species that require resources occurring in different crop types (landscape complementation).

Hyp 2b. Biodiversity **increases** with decreasing mean field size if landscapes with smaller fields also have higher density of crop edges. This could increase biodiversity measured in sampled crop fields by increasing spillover from adjacent fields or from adjacent semi-natural vegetation occurring between fields.

Hyp 2c. Biodiversity **decreases** with decreasing mean field size if most species show negative edge effects and/or if most species have minimum patch size requirements (separate from their total habitat area requirements, see Hyp1c).

Hyp 2d. Biodiversity shows a **peaked relationship** with decreasing mean field size if there is an initial increase in biodiversity for reasons explained in Hyp 2a-2b and then biodiversity decreases when mean field size reaches minimum patch size requirements for most species (Hyp 2c).

1.3. Interactions between crop compositional and configurational heterogeneity

Hyp 3a. The positive effect of crop diversity on biodiversity is **stronger** when mean field size decreases (and vice-versa) if most species require multiple land cover types easily accessible (landscape complementation). This is because increasing crop diversity increases the chance that all required crop types are available, and decreasing field sizes increases accessibility among the required crop types.

Hyp 3b. The positive effect of crop diversity on biodiversity is **weaker** when mean field size is low if most species require landscape complementation and have minimum patch size requirements. Similarly, the positive effect of decreasing mean field size on biodiversity is **weaker** when crop diversity is high if the presence of a distinct crop type in the adjacent field results in a negative edge effect for most species within the sampled field.

Hyp 3c. The positive effect of crop diversity on biodiversity is **independent** of mean field size if most species are highly mobile and can access multiple fields regardless of mean field size. The positive effect of decreasing mean field size on biodiversity is **independent** of crop diversity if most species in landscapes with low mean field size primarily benefit from an easier access to semi-natural cover, in particular to semi-natural linear elements, rather than to multiple fields.

1.4. Interactions between crop heterogeneity and semi-natural cover

Hyp 4a. The positive effect of **crop diversity** on biodiversity is **stronger** when semi-natural cover (SNC) increases if most species require complementary resources found in semi-natural cover types and several crop types (e.g. species require SNC + crop A + crop B).

Hyp 4b. The positive effect of decreasing **mean field size** on biodiversity is **stronger** when semi-natural cover (SNC) increases if most species in landscapes with low mean field size primarily benefit from an easier access to semi-natural cover, in particular to semi-natural linear elements, rather than an easier access to multiple fields.

Hyp 4c. The positive effects of crop heterogeneity on biodiversity is stronger in landscapes with **intermediate amounts of semi-natural cover** than in landscapes with very low or very high semi-natural cover (Tscharntke et al. 2012). In landscapes with no or very low semi-natural cover, species pool may be small and species may be well adapted to intensive agriculture, and biodiversity may therefore remain unaffected by crop heterogeneity levels. In landscapes with high semi-natural cover, biodiversity levels may be high everywhere due to widespread spill-over effects, and may remain unaffected by crop heterogeneity levels.

References

Allouche O, et al. (2012) Area–heterogeneity tradeoff and the diversity of ecological communities. Proc Natl Acad Sci 109(43):17495–17500.

Andreasen C, et al. (1991) Soil properties affecting the distribution of 37 weed species in Danish fields. Weed Res 31(4):181–187.

Dunning JB, et al. (1992) Ecological processes that affect populations in complex landscapes. Oikos 65(1):169–175.

Fahrig L, et al. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol Lett 14(2):101–112.

Schneider G, Krauss J, Boetzl FA, Fritze M-A, Steffan-Dewenter I (2016) Spillover from adjacent crop and forest habitats shapes carabid beetle assemblages in fragmented semi-natural grasslands. Oecologia 182(4):1141–1150.

Tscharntke T, et al. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol Rev 87(3):661–685.

Weibull A-C, et al. (2003) Species richness in agroecosystems: the effect of landscape, habitat and farm management. Biodivers Conserv 12(7):1335–1355.

SI 2 – Region and landscape selection

2.1. Region selection

We selected eight agricultural regions (Fig. S2.1) that belong to six different ecoregions (Olson et al; 2001)(51) : Eastern Great Lakes lowland forests (Eastern Ontario in Canada), Celtic broadleaf forests and English lowland beech forests (East Anglia in United Kingdom), Atlantic mixed forests (Armorique, Plaine et Val de Sèvre in France), Western European broadleaf forests (Goettingen in Germany, Coteaux de Gascogne in France), Iberian sclerophyllous and semi-deciduous forests (Lleida in Spain) and Northeastern Spain & Southern France Mediterranean forests (Camargue in France). Topography varied from flat (e.g. Camargue, Eastern Ontario) to intermediate (e.g. Goettingen, Lleida), to hilly (e.g. Coteaux de Gascogne). Climate varied from dry (e.g. Lleida) to humid (e.g. East Anglia). Complexity in crop field shapes varied from rectilinear (e.g. Camargue, Eastern Ontario) to intermediate complexity (e.g. Coteaux de Gascogne, Armorique) to complex field shapes (e.g. Lleida). Specific agricultural products were found in some regions, e.g. dairy (Armorique), olives (Lleida) or rice (Camargue). Diversity of agricultural cover types varied from low (e.g. Camargue, Lleida) to high (e.g. Coteaux de Gascogne, Plaine et Val de Sèvre). Mean field size varied from 1.2 ha in Lleida and 1.4 ha in Armorique to 4.4 ha in Eastern Ontario and 4.7 ha in East Anglia.

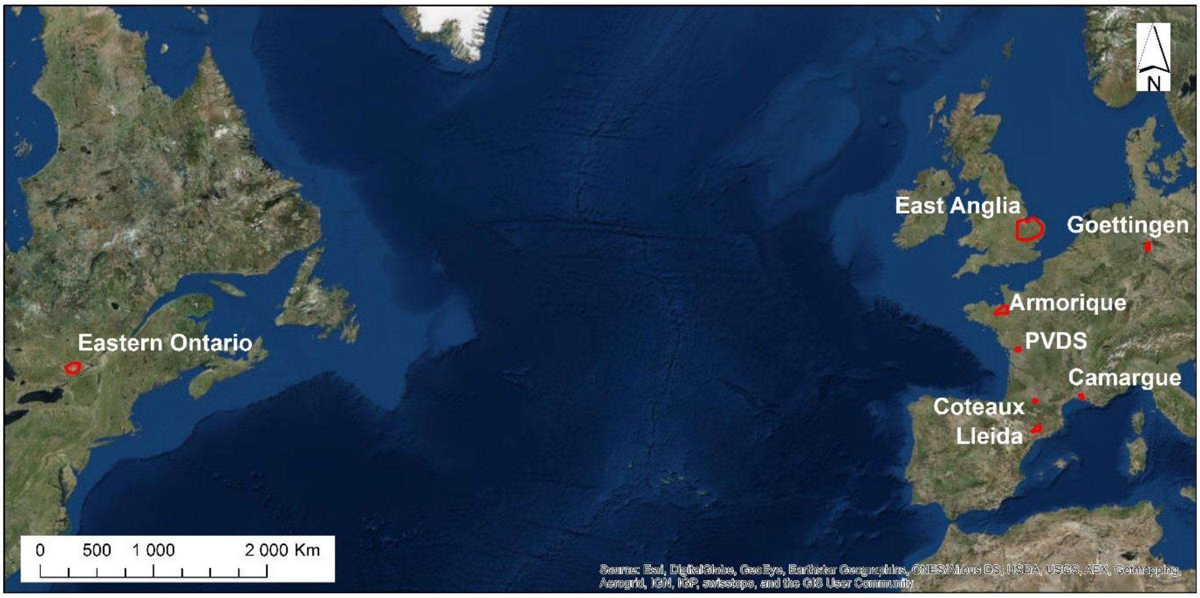


Figure S2.1. Locations of the eight study regions in Europe and North America.

2.2. Landscape selection

The purpose of the landscape selection protocol was to select in each region a set of landscapes in a pseudo-experimental design (also called a "mensurative experiment") which aimed at selecting agricultural landscapes (between 60 and 100% of agricultural cover) along two independent gradients of crop compositional and configurational heterogeneity. The general protocol is detailed in Pasher et al. (2013).

We used the highest resolution and most recent remotely sensed data or the best land cover map available within each region. We delineated all fields (contiguous production cover), even when adjacent fields contain the same agricultural cover type (as they may belong to different farmers or may be managed differently). We attributed each field to one of the following 34 agricultural cover types: cereal, fallow, alfalfa, clover, ryegrass, grassland, rice, corn, sunflower, sorghum, millet, moha, oilseed rape, mustard, pea, bean, soybean, linseed, orchard, almond, olive, vineyard, mixed vegetables, sugar beet, asparagus, carrot, onion, parsnip, potato, tomato, melon, strawberry, raspberry, wild bird cover (i.e. a spring sown crop left unharvested over winter to provide food for farmland birds). We also delineated patches of non-agricultural cover (woodland, open land, wetland and built-area).

We then calculated crop compositional heterogeneity (Shannon diversity index of the crop mosaic) and crop configurational heterogeneity (mean size of agricultural fields) as well as agricultural cover.

We selected spatially independent agricultural landscapes (between 60 and 100% of agricultural cover) within each region (Fig. S2.2), representing the maximum variation for both crop compositional heterogeneity and crop configurational heterogeneity.

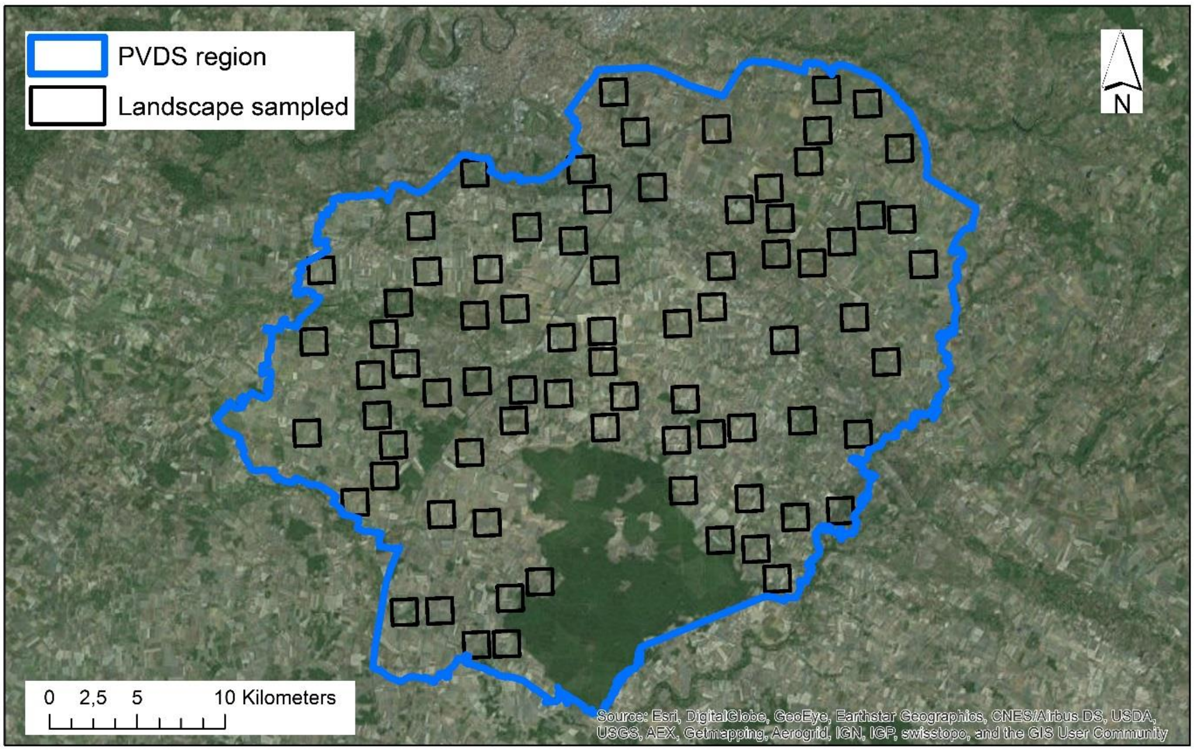


Figure S2.2. Spatial distribution of landscapes sampled in one of the eight regions (PVDS = Plaine et Val de Sèvre).

References

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. BioScience, 51, 933–938.

Pasher, J., Mitchell, S., King, D., Fahrig, L., Smith, A. & Lindsay, K. (2013) Optimizing landscape selection for estimating relative effects of landscape variables on ecological responses. Landscape Ecology, 28, 371–383.

SI 3 – Multitrophic diversity sampling

3.1. Sampling site selection

Disentangling the effects of crop diversity and mean field size on multitrophic diversity required sampling many landscapes. Trade-offs between the number of landscapes sampled and the number of sampling sites per landscape were unavoidable. Whereas studies assessing the effect of landscape structure on biodiversity are often based on a single sampling site per landscape, we decided to sample three sampling sites (i.e. three agricultural fields) within each landscape of 1 x 1 km (Fig. S3.1). These sites were located at least 200 m apart from each other, at least 50 m from the border of the 1km x 1km landscape, and at least 50 m from non-agricultural cover such as forests.

We sampled either one, two or three distinct crop types per landscape. We located these sampling sites in dominant crop types within each region. When this was not feasible, we located sampling sites in crop types available within a given landscape while limiting correlations between crop types sampled and the two heterogeneity gradients within each region (see further details in SI 5).

At each sampling site, we selected two parallel 50 m ‘transects’, one located at the field edge and the other inside the field 25 m away from the first transect (Fig. S3.2).

Figure S3.1. Example landscape showing the three selected sampling sites.

3.2. Multitrophic diversity sampling within each sampling site

Multitrophic diversity sampling occurred between 2011 and 2014 depending on the region and landscape (Table S3.1).

Table S3.1. Number of landscapes sampled and main crop types sampled within each region and each year.

Region	2011	2012	2013	2014	Total	Crop types sampled
Armorique			30	10	40	cereal, corn, grassland
Camargue			32	8	40	rice, cereal
Coteaux			20	12	32	cereal, corn, sunflower
East Anglia		30	30		60	cereal, sugar beet, oilseed rape
Goettingen			32	20	52	cereal, oilseed rape, grassland
Lleida			25	15	40	cereal, almond, olive
Eastern Ontario	46	47			93	corn, soybean, grassland

PVDS	48	48	96	cereal, grassland, oilseed rape

All taxa were sampled using sampling methods commonly used in the literature (point counts, traps, visual surveys; Fig. S3.2; Fahrig et al. 2015).

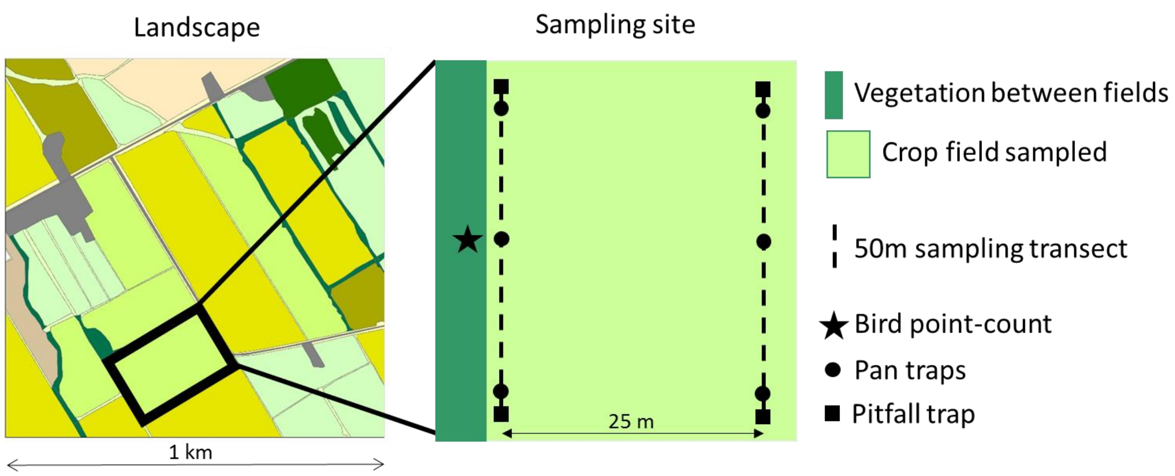


Figure S3.2. Multitrophic diversity sampling design within each sampling site within each landscape (1 km x 1 km).

While trade-offs between the number of sites sampled and sampling intensity at each site were necessary, our sampling efforts (see below: number of traps, length of transects, number of visits) were consistent with the literature (e.g. Pollard and Yates 1993, Bibby et al. 2005, Geiger et al. 2010). Table S3.2 shows the number of species and specimens we sampled for each taxa.

Table S3.2. Number of species and specimens (occurrences for plants) for each taxa.

	Species	Specimens
All taxa	2795	167028
Bees	343	13326
Birds	208	10911
Butterflies	109	10605
Carabids	256	42547
Hoverflies	146	21491
Plants	1229	30276
Spiders	504	37872

Plants - Plant surveys were conducted along the field edge and in the field interior transects. Percentage cover was recorded for each species. Each transect was 1 m wide and 50 m long and represented a total surveyed area of 20 m², except in Eastern Ontario where plant survey transects were 2m wide, represented a total surveyed area of 100 m² and the field edge transect included both the field and the boundary vegetation. Plant surveys were conducted once, except in Eastern Ontario, Goettingen and East Anglia where surveys were conducted twice.

Bees and hoverflies – Bees and hoverflies were sampled using colored pan traps, except for hoverflies in Eastern Ontario which were sampled by sweep-netting along the two transects. Plastic bowls painted in UV blue, white or UV yellow were placed in pairs at each end and at the center of each transect. As a result, we used six pan traps per transect, 12 pan traps per sampling site and 36 pan traps per landscape. The height of pan traps was adjusted to vegetation height. Cups were filled with water, with three drops of odorless soap added per 1L of water. The traps were left in the field for four days. The insects were then stored in 70 % ethanol and later identified to species level. Bee and hoverfly sampling was carried out twice during the growing season (April-July), the dates being selected in each region based on regional climatic conditions. Therefore rarefied species richness could not be calculated. Due to technical and financial constraints, bees could only be identified to species level in seven of the eight regions, and in a total of 183 landscapes. This did not affect our results (see section 3.3 of this SI).

Carabids and spiders - Carabids and spiders were sampled using pitfall traps (Bertrand et al. 2016). Cups were half-filled with a solution of 10 drops of soap and 10 g of salt per 1L of water and placed in the ground. One trap was placed at each end of each transect (two traps per transect and four per sampling site in total). The traps were left in the field for four days. Arthropods were then stored in 70 % ethanol and carabids and adult spiders were later identified to species level. Carabids and spiders were sampled at the same time as the bee and hoverfly sampling (above). They were carried out only once in East Anglia in 2012 due to bad weather conditions and could not be conducted in rice fields in Camargue due to the presence of water.

Butterflies - Butterfly surveys were conducted along the field edge and in the field interior transects (Pollard and Yates 1993). Surveys were conducted on calm (Beaufort scale < 3), sunny days, when the temperature was > 15°C. The observer recorded all butterfly species observed within an imaginary 5 m-sided box (2.5 m to each side, 5 m in front and 5 m high) during approximately 10 min per transect (Pollard and Yates 1993). Individuals that could not be identified by sight were captured with a butterfly net for closer examination (survey time was stopped during capture and identification). Surveys were conducted once, except in Eastern Ontario, Goettingen and Lleida were surveys were conducted twice.

Birds - Birds were surveyed using 10-minutes point counts (Bibby et al. 2005) located at the center of the border transect. All individuals singing or seen within a distance of 100m were recorded. Birds flying across were considered as transients and thus not included. Counts were conducted twice, except in East Anglia in 2012 due to bad weather conditions, in Ontario and in rice fields in Camargue due to the specific phenology of this crop type, where they were conducted once. Surveys were conducted during the peak breeding season, between April and June depending on the region, and during peak activity hours, from 1 to 4 hours after sunrise and under good weather conditions.

Note on detection and rare species – Our sampling scheme presents the following characteristics : 1) the three fields within each landscape often correspond to different crop types and therefore correspond to different species pools; 2) we only sampled each landscape during a single year; 3) we sampled some taxa across two sessions within the sampling season but these sessions target distinct communities (e.g. spring versus summer spider communities); 4) some protocols involve multiple sampling within the field (e.g. several pitfall traps along the edge transect and several pitfall traps along the center transect) but these traps cannot be considered as replicates due to the high level of heterogeneity within fields, both between transects and within a transect. As a result, we do not think we have truly replicated data that would allow us computing species richness estimators such as the Chao estimator. Nevertheless, because we used standard protocols commonly used in the literature, we believe that when pooling the data at the landscape level, our uncorrected data is a good proxy of species richness for each taxa studied.

3.3. Multidiversity

An important challenge when studying the overall effects of crop heterogeneity on multitrophic diversity is that different taxa might respond differently (Flynn et al. 2009; Kormann et al. 2015; Concepción 2016). Indeed, we observed weak correlations among taxa within our dataset (Table S3.3) and significant differences in the response of taxa (Fig. 4 in the main text).

Table S3.3. Mean species richness per landscape ± standard deviation for each taxa and correlations among taxa (Pearson correlation coefficients). * p<0.05; ** p<0.01; *** p<0.001.

	Mean SR	birds	bees	butterflies	carabids	hoverflies	plants
birds	18.7±6.7						
bees	11.2±4.6	0.11					
butterflies	5.4±2.9	0.03	0.14				
carabids	12.3±6.8	0.01	-0.18*	0.13**			
hoverflies	6.4±3.7	-0.04	0.14	0.09	0.25		
plants	44.9±17.5	0.19	-0.07	0.23	-0.21	0.12	
spiders	20.6±11.5	0.17*	0.41***	-0.20**	0.34***	0.16***	-0.27

To test the overall effects of crop heterogeneity on multitrophic diversity, we investigated methods developed by Allan et al. (2014) to study ecosystem multifunctionality. Such approach differs from testing how crop heterogeneity impacts each taxa separately by searching for optimal landscape conditions that promote most taxa simultaneously.

A first approach to achieve this is to calculate a multidiversity index based on the averaged approach (Byrnes et al. 2014). This approach consists simply in calculating the average standardized values of multiple taxonomic diversities for each landscape, as follows:

$$\text{Average-based Multidiversity} = \frac{1}{7} \times \sum_{i=1}^{n=7} \text{scale}(SR_i\text{, center=T, scale=T})$$

where SR_i is the number of species for taxa i in a given landscape.

Although this averaging approach provides an intuitive method to assess changes in diversity across multiple taxa simultaneously (Allan et al. 2014), the averaged-approach includes some biases. For instance, very high averaged-multidiversity values implies that all groups exhibit high diversity. However, intermediate averaged-multidiversity values are difficult to interpret and it is impossible to differentiate situations where (i) diversity values are intermediate for all taxa simultaneously; or (ii) diversity values are very high for some groups while they are very low for others, i.e. trade-offs among taxa (Byrnes et al. 2014).

To overcome this limitation, we used a threshold approach (Zavaleta et al. 2010) not biased by potential trade-offs among taxa (Byrnes et al. 2014). The objective of this approach is to assess the ability of agricultural landscapes to simultaneously host at least a given percentage, or threshold (x), of the maximum species richness observed for each taxa (SRmax). Because SRmax is likely to vary between regions, we chose to use the 95th percentile of the maximum observed species richness within each region as SRmax.region for each taxa. We then calculated the multidiversity index based on the following formula:

$$\text{Threshold} - \text{based Multidiversity (Tx.landscape)} = \frac{1}{7}\sum_{i=1}^{n=7}(\text{SR i} > (x \times \text{SRmax.region j}))$$

where SR_i is the number of species for taxa i, x is the minimum % to reach and SRmax.region is the maximum species richness for group i in the region the landscape considered belong to. For a given taxon, if SR_i is above the threshold, this taxon is associated with the value 1. The sum ranges between 0 and 7, and the multidiversity index ranges between 0 and 1.

We calculated this multidiversity index for each threshold x between 20 and 90% (every 10%). For each threshold x, the multidiversity index was smoothed by calculating the average over the interval [x − 10%, x + 10%] (Le Bagousse-Pinguet et al. 2019). It is recommended to focus on intermediate thresholds since care should be taken to avoid over-interpreting high or low thresholds (Lefcheck et al. 2015) and intermediate thresholds have been shown to provide an effective measure of multitrophic diversity in agricultural landscapes (Byrnes et al. 2014). We chose to focus our analyses on the threshold of 60% after checking that the distribution of T60.landscape allows developing robust linear statistics (Fig.S3.3).

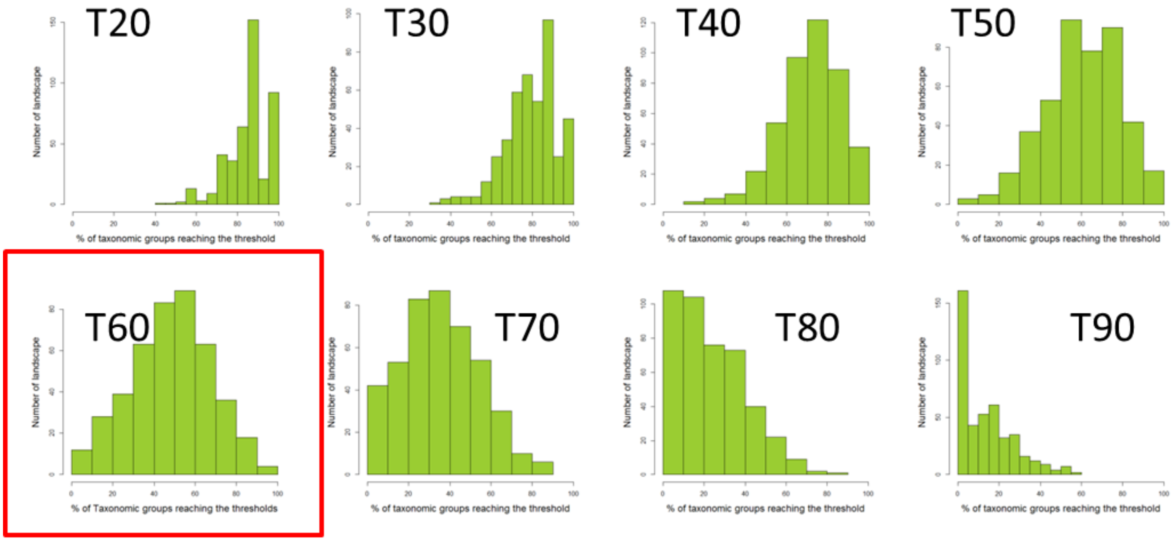


Figure S3.3. Distribution of the threshold-based multitrophic diversity calculated at the landscape level for thresholds between 20 and 90%.

A high multidiversity value based on a threshold of 60% means that most taxa are associated with species richness levels higher than 60% of the regional maximum (SRmax.region) observed in our study. Note that (i) T60.landscape was highly correlated with the averaged multidiversity index in our dataset and other threshold-based multidiversity indices (Table S3.4) (ii) our results were not sensitive to the threshold selected (Fig. S5.1 in SI 5).

Table S3.4. Correlation between average-based multidiversity (M), various threshold-based multidiversity indices calculated at the landscape level (T) and species richness for each taxa. Colors correspond to increasing correlation values (from orange to dark red).

	M	T20	T30	T40	T50	T60	T70	T80	Plant	Bee	Syrphid	Butterfly	Carabid	Spider	Bird
M	1	0.48	0.60	0.71	0.80	0.86	0.88	0.86	0.51	0.59	0.39	0.54	0.56	0.64	0.37
T20	0.48	1	0.92	0.77	0.65	0.58	0.52	0.47	0.08	0.19	0.23	0.21	0.07	0.22	0.61
T30	0.60	0.92	1	0.93	0.79	0.69	0.62	0.56	0.15	0.31	0.23	0.28	0.21	0.31	0.59
T40	0.71	0.77	0.93	1	0.93	0.82	0.74	0.66	0.23	0.45	0.27	0.34	0.33	0.40	0.54
T50	0.80	0.65	0.79	0.93	1	0.94	0.85	0.74	0.32	0.54	0.28	0.39	0.41	0.48	0.50
T60	0.86	0.58	0.69	0.82	0.94	1	0.95	0.84	0.38	0.57	0.28	0.44	0.45	0.54	0.46
T70	0.88	0.52	0.62	0.74	0.85	0.95	1	0.95	0.42	0.54	0.29	0.45	0.46	0.59	0.43
T80	0.86	0.47	0.56	0.66	0.74	0.84	0.95	1	0.42	0.48	0.29	0.43	0.45	0.57	0.44
Plant	0.51	0.08	0.15	0.23	0.32	0.38	0.42	0.42	1	0.04	0.01	0.22	0.21	0.18	0.00
Bee	0.59	0.19	0.31	0.45	0.54	0.57	0.54	0.48	0.04	1	0.25	0.24	0.19	0.30	0.12
Syrphid	0.39	0.23	0.23	0.27	0.28	0.28	0.29	0.29	0.01	0.25	1	0.07	0.06	0.06	-0.06
Butterfly	0.54	0.21	0.28	0.34	0.39	0.44	0.45	0.43	0.22	0.24	0.07	1	0.14	0.20	0.03
Carabid	0.56	0.07	0.21	0.33	0.41	0.45	0.46	0.45	0.21	0.19	0.06	0.14	1	0.34	-0.02
Spider	0.64	0.22	0.31	0.40	0.48	0.54	0.59	0.57	0.18	0.30	0.06	0.20	0.34	1	0.15
Bird	0.37	0.61	0.59	0.54	0.50	0.46	0.43	0.44	0.00	0.12	-0.06	0.03	-0.02	0.15	1

Data for bee species richness were only available for 183 landscapes. To determine whether this affected our results, we also calculated the multidiversity index across six taxa (all groups except bees). As there was no difference in results obtained with six or seven taxa, we here only present results for the multidiversity index calculated across seven taxa within 435 landscapes.

References

Allan E, et al. (2014) Interannual variation in land-use intensity enhances grassland multidiversity. Proc Natl Acad Sci U S A 111(1):308–313.

Bertrand C, Burel F, Baudry J (2016) Spatial and temporal heterogeneity of the crop mosaic influences carabid beetles in agricultural landscapes. Landsc Ecol 31(2):451–466.

Bibby, C.J., et al. (2005) Bird Census Techniques. Academic Press, London, UK.

Byrnes JEK, et al. (2014) Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. Methods Ecol Evol 5(2):111–124.

Concepción ED, et al. (2016) Contrasting trait assembly patterns in plant and bird communities along environmental and human-induced land-use gradients. Ecography 40(6):753-763.

Fahrig L, et al. (2015) Farmlands with smaller crop fields have higher within-field biodiversity. Agric Ecosyst Environ 200:219–234.

Flynn DFB, et al. (2009) Loss of functional diversity under land use intensification across multiple taxa. Ecol Lett 12(1):22–33.

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W. W., Emmerson, M., Morales, M. B.,… & Eggers, S. (2010). Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic and Applied Ecology, 11(2), 97-105.

Kormann U, et al. (2015) Local and landscape management drive trait-mediated biodiversity of nine taxa on small grassland fragments. Divers Distrib 21(10):1204–1217.

Le Bagousse-Pinguet Y, et al. (2019) Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality. Proc Natl Acad Sci:201815727.

Lefcheck JS, et al. (2015) Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nat Commun 6:6936.

Pollard, E., Yates, T.J. (1993). Monitoring butterflies for ecology and conservation. Chapman et Hall, London.

Zavaleta ES, Pasari JR, Hulvey KB, Tilman GD (2010) Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. Proc Natl Acad Sci U S A 107(4):1443–1446.

SI 4 – Land cover mapping and landscape metrics

4.1. Land cover mapping

Land cover was mapped based on remotely-sensed data and ground-truthing. All cover types, including fields, linear elements between fields and non-agricultural cover types, were mapped as polygons ('patches') (Fig. S4.1). We here refer to 'cover types' rather than 'habitats' because 'habitat' refers to the specific ecological requirements of a given species while 'cover type' refers to a category of land cover without any assumption on species use. This is important in the present study where we assume that many farmland species are likely to use several cover types (landscape complementation).

Agricultural cover types included: cereal, fallow, alfalfa, clover, ryegrass, rice, corn, sunflower, sorghum, millet, moha, oilseed rape, mustard, pea, bean, soybean, linseed, orchard, almond, olive, vineyard, mixed vegetables, sugar beet, asparagus, carrot, onion, parsnip, potato, tomato, melon, strawberry, raspberry, wild bird cover, grassland (including temporary and permanent grassland managed for production purpose) and other crops (unknown or rare crops). We chose to include managed grassland within agricultural cover types because we were interested in assessing the role of spatial heterogeneity within the farmed part of the landscape. We considered grasslands where more than 50% of the biomass was removed as agricultural cover whereas those where less than 50% of the biomass was removed were considered as non-agricultural cover. Linear elements between fields were classified either as woody, grassy, water (e.g. ditches) or tracks. Non-agricultural cover types included woodland (including woody linear elements), open land (e.g. shrubland, grassy linear elements), wetland and built-area (including roads).

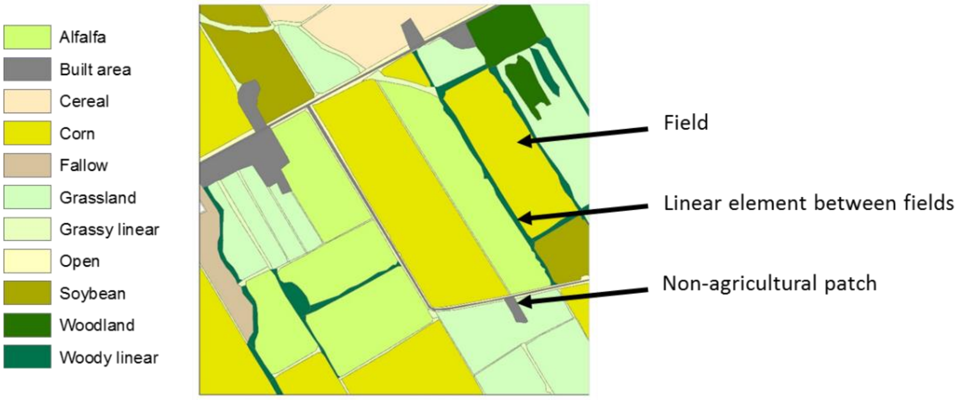


Figure S4.1. Example of land cover map used to calculate variables within each landscape (1km x 1km).

4.2. Landscape metrics

It is well known that different taxa and even species are likely to respond to the landscape structure at different spatial scales. Since our aim was to assess the overall effects of crop diversity and mean field size on a range of contrasted taxa, we chose to calculate landscape variables within a 1x1 km because this spatial extent represent the best compromise between highly mobile taxa (e.g. birds) and taxa with more limited dispersal abilities (e.g. plants or spiders; Kormann et al. 2015).

4.2.1. Number of crop types sampled

The number of crop types sampled ranged from one to three. The diversity of crop types available in the landscape and the number of crop types sampled within each landscape were not heavily correlated (r=0.45).

4.2.2. Crop compositional heterogeneity

We used the diversity of crop types available in the landscape (hereafter ‘crop diversity’) as a measure of crop compositional heterogeneity. We measured crop diversity using the Shannon diversity index, a widely used metric of landscape heterogeneity (e.g. Bertrand et al. 2016; Bosem Baillod et al. 2017): $H' = -\sum_{i=1}^{n} p_i \ln p_i$ where p_i is the proportion of crop type i in the agricultural mosaic. Note that this metric assumes that all agricultural cover types (defined in 4.1) are considered equally different. This variable does not take into account within-field crop heterogeneity, e.g. intercropping patterns.

The diversity of crop types available in the landscape and the number of crop types sampled within each landscape were not heavily correlated (r=0.45).

4.2.3. Crop configurational heterogeneity

We used mean field size (ha) as a measure of crop compositional heterogeneity. We chose this metric over total field perimeter length per landscape (e.g. Bosem Baillod et al. 2017) because it is directly related to our hypotheses (see SI 1). Moreover it is easier to base practical recommendations for future agricultural policies on mean field size rather than on total field perimeter length. Fields were only mapped within the 1 km² landscape. As a result, for fields located partly outside of the 1 km² landscape, only their area contained within the landscape was considered in calculating mean field size. This may lead to a slight underestimation of mean field size.

4.2.4. Semi-natural cover proportion

We calculated the sum of woodland (including woody linear elements), open land (e.g. shrubland, grassy margins) and wetland cover (including ponds, rivers, ditches) in the landscape.

4.2.5. Total length of semi-natural linear elements

We assessed the total length of vegetation occurring in semi-natural linear elements between fields (SNL, in meters) by calculating half the sum of all semi-natural linear elements located between two fields (e.g. hedgerows, grassy margins). Note that semi-natural linear elements located along roads or urban areas were not included in the calculation of SNL. SNL and mean field size were highly correlated (see Table S5.5. in SI 5).

4.2.6. Latitude and longitude

We calculated the latitude and longitude of the center of each landscape using the WGS 1984 World Mercator projection system.

4.3. Descriptive statistics for the 435 landscapes selected

The 435 landscapes selected across eight regions of Europe and North America had the following characteristics (mean ± sd; see also Table S4.1): 1.94±0.56 crop types sampled, 81.3±9.6 % of agricultural cover, 12.7±8.9 % of semi-natural cover, 5631±3822 m of linear semi-natural elements between fields, mean field size 2.99±2.02 ha and a Shannon diversity index of agricultural cover types of 1.03±0.39 (Fig S4.3). These gradients are representative of most Western European agricultural landscapes (Herzog et al. 2006) and most American agricultural landscapes (Yan & Roy 2016).

Table S4.1. Descriptive statistics for each landscape variable (mean, median, 25th and 75th quartiles, min and max): number of crop types sampled (Crop nb), diversity of crop types available in the landscape (Crop diversity), mean field size (ha), the percentage of semi-natural cover types (SNC), and the length of semi-natural linear elements (SNL).

	Crop nb	Crop diversity	Mean field size (ha)	SNC (%)	SNL (m)

Min	1	0.0	0.48	0.0	0
1st quartile	2	0.8	1.71	6.0	3108
Median	2	1.09	2.43	10.9	4824
Mean	1.94	1.03	2.99	12.7	5632
3rd quartile	3	1.31	3.69	17.6	7370
Max	3	2.03	12.71	49.5	27989

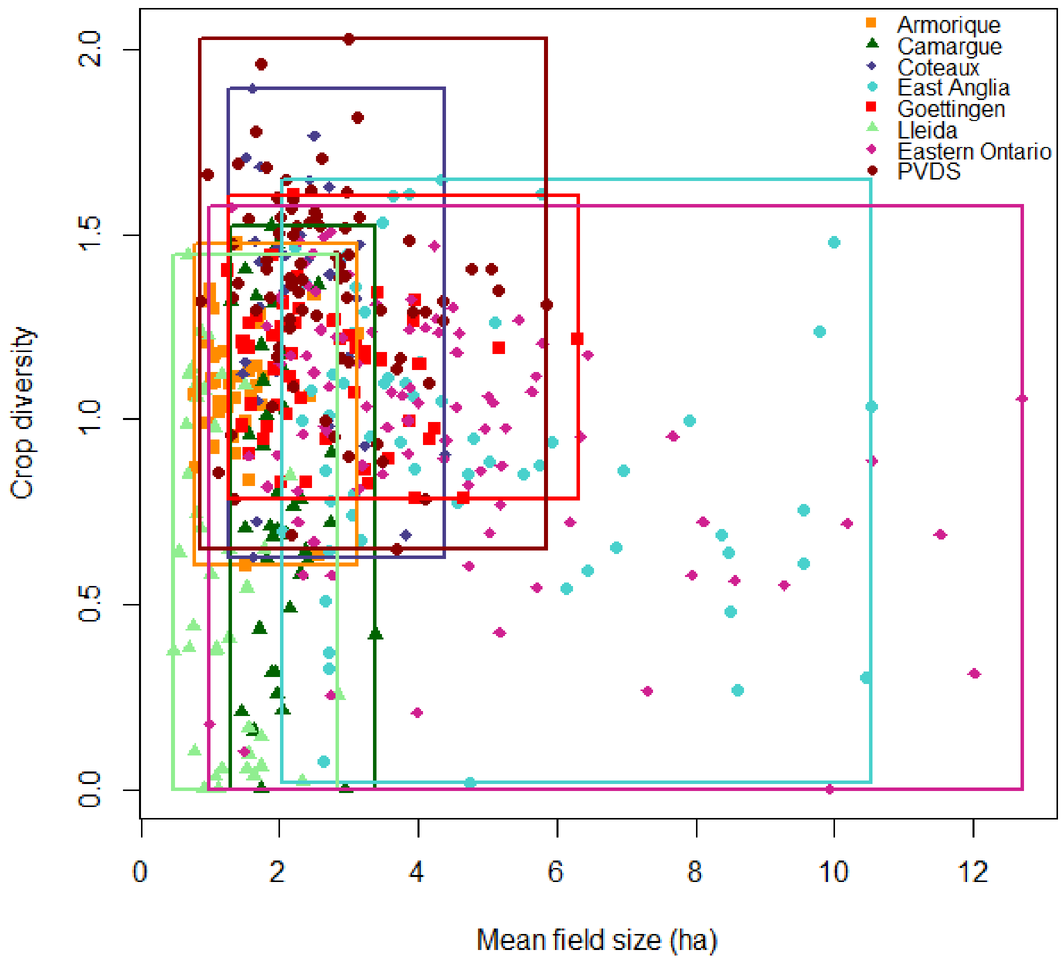


Figure S4.3. Variation in crop diversity and mean field size (ha) across the eight regions. Points correspond to selected landscapes (N= 435) and boxes corresponds to the range of crop diversity and mean field size sampled within each region (orange=Armorique, dark green=Camargue, dark blue=Coteaux, light blue=East Anglia, light red=Goettingen, light green=Lleida, pink=Eastern Ontario, dark red=PVDS).

4.4. Effects of the number of crop types sampled vs. the diversity of crop types in the landscape

Biodiversity may increase with increasing crop diversity if different crop types can serve as habitat for different specialized species (single habitat specialization; Fig. S4.4). In that case, sampling more crop types will result in higher observed landscape-level multitrophic diversity. Biodiversity may also increase with crop diversity if different crop types provide different resources required for single species (landscape complementation). In that case, sampling the same number of crop types in landscapes with higher crop diversity will result in higher landscape-level multitrophic diversity.

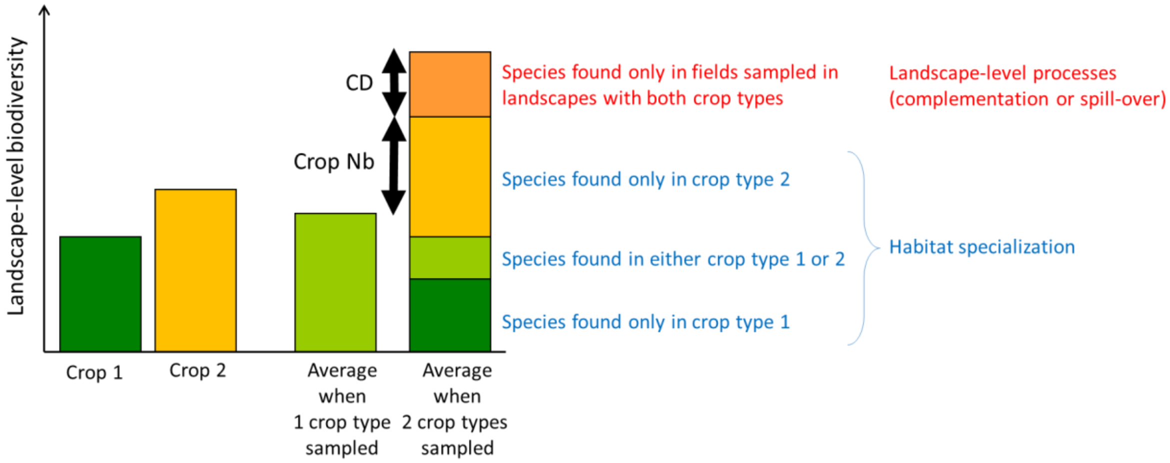


Figure S4.4. Roles of habitat specialization, landscape complementation or spill-over in the potential positive effect of crop diversity on multitrophic diversity (see SI 1). Black arrows represent the effect of our two explanatory variables (CD = increasing the diversity of crop types in the landscape; Crop Nb = increasing the number of crop types sampled).

Since the diversity of crop types available in the landscape and the number of crop types sampled within each landscape were not heavily correlated (r=0.45), we were able to disentangle the role of these two mechanisms (Fig. S4.5).

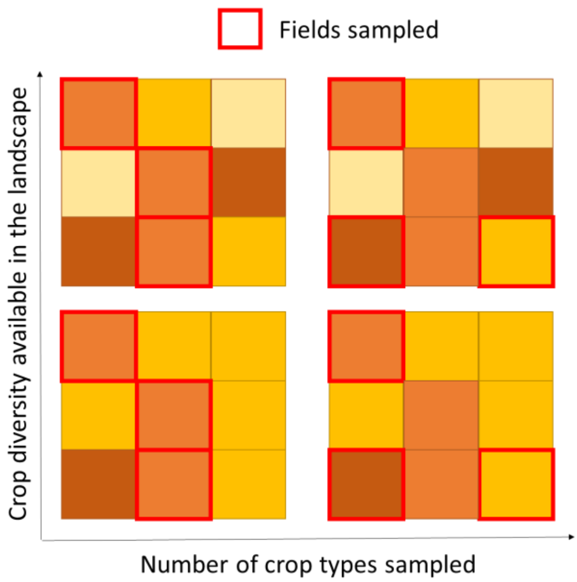


Figure S4.5. Representation of our sampling design allowing us to take into account the potential contribution of habitat specialization and landscape complementation/spillover to the positive effect of crop diversity on multitrophic diversity.

References

Bertrand C, Burel F, Baudry J (2016) Spatial and temporal heterogeneity of the crop mosaic influences carabid beetles in agricultural landscapes. Landsc Ecol 31: 451–466.

Bosem Baillod A, Tscharntke T, Clough Y, Batáry P (2017) Landscape-scale interactions of spatial and temporal cropland heterogeneity drive biological control of cereal aphids. J Appl Ecol, 54: 1804-1813.

Herzog F, et al. (2006) Assessing the intensity of temperate European agriculture at the landscape scale. Eur J Agron 24(2): 165–181.

Kormann U, et al. (2015) Local and landscape management drive trait-mediated biodiversity of nine taxa on small grassland fragments. Divers Distrib 21(10):1204–1217.

Yan, L. & Roy, D.P. (2016) Conterminous United States crop field size quantification from multi-temporal Landsat data. Remote Sensing of Environment, 172: 67–86.

SI 5 – Complementary analyses

5.1. Details of the model selection and model averaging for multitrophic diversity

We first tested the effect of crop heterogeneity on multitrophic diversity (Model 1).

*Model 1: lmer (T60.landscape ~ CD * MFS * SNC + CD^2 + MFS^2 + SNC^2 + CropNb + Lat + Lon + (1| Region/Year))*

The model selection approach based on ΔAICc<2 resulted in the selection of 10 sub-models (Table S5.1). Using a ΔAICc of 7 did not change the results of the model averaging or results on variable importance. All models included crop diversity (CD), mean field size (MFS), semi-natural cover (SNC), the number of crops sampled per landscape (Crop nb) and the interaction between crop diversity and semi-natural cover (CD x SNC). The AICc of the Null model was 3709 while the AICc of the best model was 3667, i.e. a ΔAICc of 42, suggesting that the best selected models were far more parsimonious than the null model including only Region and Year as random effects.

Table S5.1. List of all sub-models selected and used for the model averaging approach for model 1.

Sub-model	1-1	1-2	1-3	1-4	1-5	1-6	1-7	1-8	1-9	1-10	Null
Lat								x			
Lon				x	x		x		x		
CD	x	x	x	x	x	x	x	x	x	x	
CD^2										x	
MFS	x	x	x	x	x	x	x	x	x	x	
MFS^2	x	x		x	x			x		x	
SNC	x	x	x	x	x	x	x	x	x	x	
Crop nb.	x	x	x	x	x	x	x	x	x	x	
CD x SNC	x	x	x	x	x	x	x	x	x	x	
MFS x SNC		x			x	x			x		
CD xMFS x SNC											
Marginal R^2	0.13	0.13	0.12	0.15	0.15	0.12	0.14	0.12	0.14	0.13	0
Conditonal R^2	0.36	0.37	0.35	0.38	0.38	0.36	0.37	0.37	0.37	0.36	0.23
df	10	11	9	11	12	10	10	11	11	11	–
AICc	3667.5	3668.09	3668.16	3668.21	3668.75	3668.75	3668.86	3669.36	3669.39	3669.56	3709.7
delta	0	0.59	0.66	0.7	1.24	1.24	1.35	1.85	1.89	2.05	42.23
weight	0.17	0.13	0.12	0.12	0.09	0.09	0.09	0.07	0.07	0.06	–

5.2. Influence of selected threshold on parameter estimates for multitrophic diversity

To test whether the choice of threshold for computing the multitrophic diversity index impacted our conclusions, we ran model 2 for all thresholds from T20 to T80 (i.e. proportion of taxa for which the species richness is equal to or higher than 20% to 80% of the regional maximum species richness per landscape).

Parameters estimates were consistent across the range of thresholds (Fig. S5.1). Moreover, variations in parameter estimates suggests that increasing mean field size may be particularly effective to reach intermediate multidiversity thresholds (i.e. between 30 and 50% of regional maximum) whether increasing semi natural cover may be effective to reach higher multidiversity threshold (i.e. above 50% of regional maximum).

This comparison confirms the validity of choosing T60.landscape, i.e. the proportion of taxa for which the species richness is equal or higher than 60% of the regional maximum species richness per landscape.

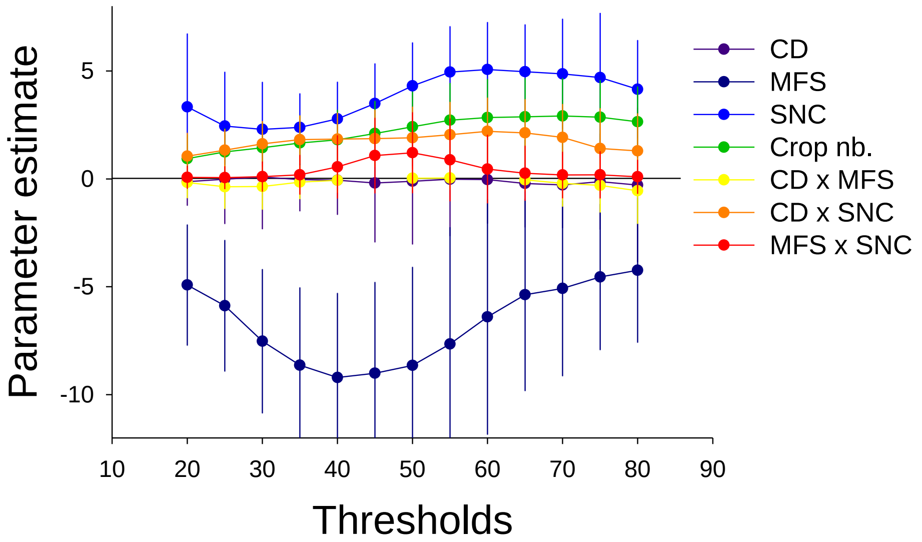


Figure S5.1. Parameter estimates based on model 1 for different thresholds. Thresholds correspond to the % of SR max used to calculate the multidiversity index. In this paper, we present model outcomes for a threshold of 60%, i.e. we use the proportion of taxa that exceeded 60% of the maximum species richness.

5.3. Variation in the response of multitrophic diversity among regions

To test whether the effects of crop diversity, mean field size and semi-natural cover on multitrophic diversity measured at the landscape level (T60.landscape) varied significantly among regions we added random effects for region on the slopes of crop diversity, mean field size, semi-natural cover as well as the interaction between crop diversity and semi-natural cover (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 crop diversity, mean field size, semi-natural cover as well as the interaction between crop diversity and semi-natural cover, we used the function exactRLRT from package RLRsim.

*Model 2: lmer (T60.landscape ~ CD * MFS * SNC + CD² + MFS² + SNC² + CropNb + Lat + Lon + (1|Region/Year) + (0+CD|Region)) + (0+MFS|Region) + (0+SNC|Region) + (0+CD:SNC|Region))*

Table S5.2. Comparison of model 1 and model 2 (i.e. model including a random effect of region on slope). Parameter listed are those retained in the model selection procedure. Parameter estimates and confidence intervals are based on the model averaging approach. ° p<0.1; * p<0.05; ** p<0.01; *** p<0.001.

	model 1	model 2
Crop diversity (CD)	-0.03 [-2.07 ; 2.01]	-0.16 [-2.22 ; 1.9]
Mean field size (MFS)	-6.39 [-11.85 ; -0.94] *	-5.22 [-11.29 ; 0.85] °
Semi-Natural Cover (SNC)	5.07 [2.87 ; 7.26] ***	4.35 [0.79 ; 7.91] *
Nb of Crops sampled	2.84 [1.07 ; 4.62] ***	3.05 [1.29 ; 4.8] ***
Latitude	1.5 [-3.55 ; 6.55]	
Longitude	3.73 [2.47 ; 9.93]	-2.39 [-8.39 ; 3.62]
MFS²	3.78 [-0.67 ; 8.23] °	3.78 [-2.26 ; 9.83]
SNC²		-2.39 [-8.39 ; 3.62]
CD :SNC	2.20 [0.64 ; 3.76] **	2.06 [0.29 ; 3.82] *
MFS :SNC	1.15 [-0.66 ; 2.96]	1.51 [-0.44 ; 3.46]

The random effect of region on the slope of MFS was significant in model 2 (RLRT = 3.28, p=0.02) whereas the effects on CD (RLRT=0, p=1), SNC (RLRT=0.04, p=0.33) and CD:SNC (RLRT=0.19, p=0.24) were not (Fig. 4). This result confirms that the regional context can modulate the effect of mean field size on multitrophic diversity, but that the positive effects of increasing CD, when SNC is high enough, and decreasing MFS remain valid across all regions (Table S5.2).

5.4. Results on the species richness of taxonomic groups

We tested the effects of crop heterogeneity on the species richness of taxonomic groups (Model 3). To do this, we fitted a similar model, using the landscape-level species richness of taxonomic groups (SR) as the response variable. To reflect that species pools vary between taxa, we added Taxon as a random effect.

Model 3: $lmer\ (SR \sim CD*MFS*SNC + CD^2 + MFS^2 + SNC^2 + CropNb + Lat + Lon + (1|Region/Year) + (1|Taxon))$

The effects of crop heterogeneity on the species richness of taxonomic groups were similar to their effects on multitrophic diversity (Fig. S5.2).

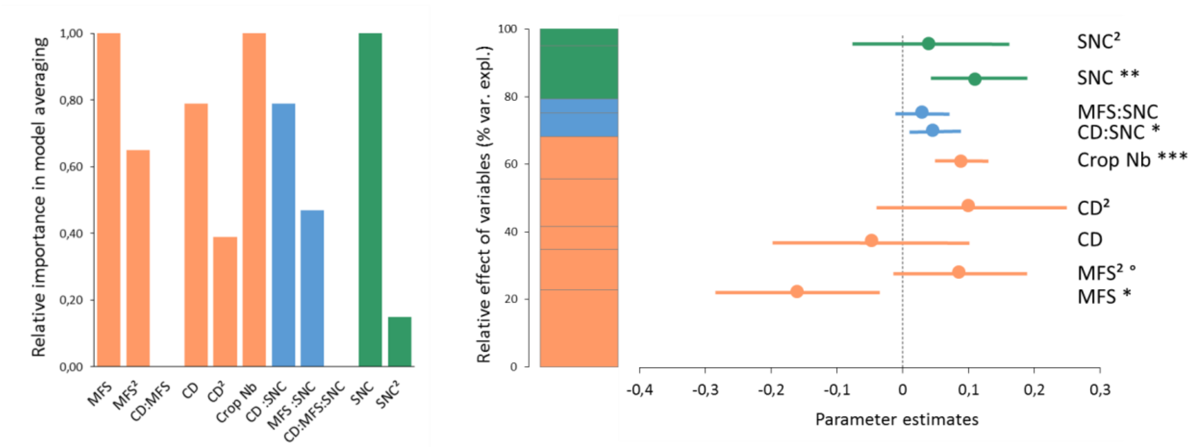


Figure S5.2. Response of the species richness of taxonomic groups to the diversity of crop types available within the landscape (CD), the number of crops sampled (Crop Nb), mean field size (MFS), semi-natural cover (SNC), and interaction terms (CD:SNC, MFS:SNC, see further details in Methods), based on data collected in 435 landscapes located in eight agricultural regions. Covariates (Lon, Lat) were excluded from the figure for simplicity. Importance of each variable in the model averaging approach (model 3), estimated as the proportion of models where the variable was selected. The relative effect of each variable corresponds to the ratio between its parameter estimate and the sum of all parameter estimates (i.e. the % of variance explained). Parameter estimates and confidence intervals, based on a model averaging approach applied to model 3 (Methods). ° p<0.1; * p<0.05; ** p<0.01; *** p<0.001. Variables are grouped in three components: orange = crop heterogeneity (MFS, MFS^2, CD, CD^2, MFS:CD, Crop Nb), green = semi-natural cover (SNC, SNC^2), blue = interactive effects between crop heterogeneity and semi-natural cover (CD:SNC, MFS:SNC, CD:MFS:SNC).

To test whether the effects of crop diversity, mean field size and semi-natural cover on the species richness of taxonomic groups varied significantly among taxa we added random effects for Taxon on the slopes of crop diversity, mean field size, semi-natural cover as well as the interaction between crop diversity and semi-natural cover (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 crop diversity, mean field size, semi-natural cover or the interaction between crop diversity and semi-natural cover, we used the function exactRLRT from package RLRsim.

*Model 4: lmer (SR ~ 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))*

Table S5.3. Comparison of model 3 and model 4 (i.e. model including a random effect of taxa on slopes). Parameter listed are those retained in the model selection procedure. Parameter estimates and confidence intervals are based on the model averaging approach. ° p<0.1; * p<0.05; ** p<0.01; *** p<0.001.

	model 3	model 4
Crop diversity (CD)	-0.05 [-0.2 ; 0.11]	-0.05 [-0.21 ; 0.1]
Mean field size (MFS)	-0.16 [-0.28 ; -0.04] *	-0.14 [-0.26 ; -0.03] *
Semi-Natural Cover (SNC)	0.11 [0.04 ; 0.18] **	0.11 [0.06 ; 0.17] ***
Nb of Crops sampled	0.09 [0.05 ; 0.13] ***	0.09 [0.05 ; 0.13] ***
Latitude	0.07 [-0.03 ; 0.16]	0.06 [-0.03 ; 0.16]
CD^2	0.1 [-0.04 ; 0.24]	0.08 [-0.07 ; 0.23]
MFS^2	0.08 [-0.02 ; 0.19] °	0.07 [-0.03 ; 0.17]
SNC^2	0.04 [-0.08 ; 0.16]	0.01 [-0.11 ; 0.13]
CD :SNC	0.04 [0.01 ; 0.08] *	0.05 [0.002 ; 0.09] *
MFS :SNC	0.03 [-0.01 ; 0.07]	0.03 [-0.01 ; 0.07]

The random effect of taxa on the slope of CD (RLRT = 1.94, p=0.06), MFS (RLRT=0.05, p=0.34), SNC (RLRT=0.26, p=0.24) and CD:SNC (RLRT=0.35, p=0.22) were not significant in model 4 (Fig. 5). This result confirms that the effects of crop heterogeneity on species diversity vary only marginally among taxa, and that the positive effects of decreasing mean field size, increasing the number of crop sampled, increasing semi-natural cover, and when semi-natural cover is high, increasing crop diversity, remain valid across all taxa (Table S5.3).

5.5. Correlations and alternative mechanisms at the landscape level

Crop diversity and mean field size are likely to be correlated with several variables, including the overall composition of the crop mosaic, the proportion of grassland in the mosaic or the length of semi-natural vegetation occurring between fields. Disentangling the role of crop heterogeneity from the effects of these other variables is necessary in order to infer potential mechanisms explaining the positive effect of crop heterogeneity on multitrophic diversity. In the present study, some of these additional variables were correlated among themselves, or with our variables of interest. Exploring their role sometimes required running models using a data subset for which relevant variables were uncorrelated. As a result, we could not include all these variables in a single model and present these analyses as separate, complementary analyses.

5.5.1. Role of the identity of crops in the agricultural mosaic

The identity of crop types in the mosaic may vary along the gradients of crop diversity and mean field size. For instance, landscapes with small fields may be composed of more biodiversity-friendly crops. Such a correlation would represent a potential bias in our study and hamper our ability to test the effects of crop heterogeneity on multitrophic diversity.

We investigated the correlation between each crop heterogeneity gradient and the identity of crop types in the mosaic for 435 landscapes from 8 regions. We conducted a Principal Components

Analysis on the matrix of percentage cover per agricultural cover type per landscape. The first axis represented 40% of the variance, while the second axis represented 19% of the variance.

The Pearson correlations between crop diversity and the first two axes of the PCA were weak (axis 1: r=-0.03, p=0.56 and axis 2: r=-0.19, p<0.001), as were the Pearson correlations between mean field size and the first two axes of the PCA (axis 1: r=0.21, p<0.001 and axis 2: r=-0.12, p=0.01; Fig. S5.3).

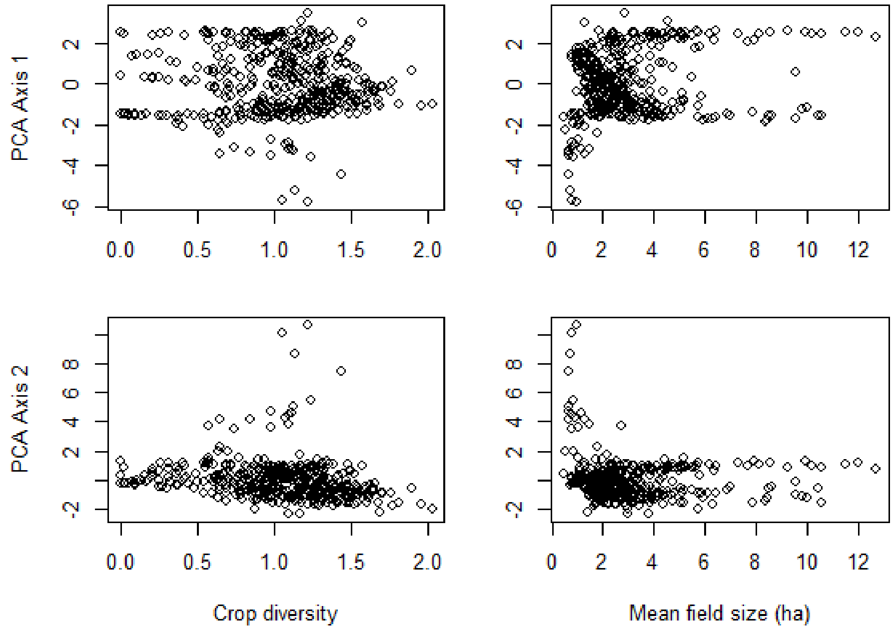


Figure S5.3. Relationships between the two crop heterogeneity gradients and the identity of crop types in the mosaic (axes 1 and 2 of the Principal Components Analysis).

We added the scores of landscapes along axes 1 and 2 of the PCA to model 1 and compared the outcomes of the obtained model (model 3) with those of model 1.

Model 1: $lmer (T60.landscape \sim CD * MFS * SNC + CD^2 + MFS^2 + SNC^2 + CropNb + Lat + Lon + (1| Region/Year))$

Model 5: $lmer (T60.landscape \sim CD * MFS * SNC + CD^2 + MFS^2 + SNC^2 + CropNb + Lat + Lon + Axis1 + Axis\ 2 + (1| Region/Year))$

The average model selected based on model 5 included the same variables as the average model selected based on model 1, plus variable PCA Axis 1. Parameter estimates and significance for variables of interest remained unchanged (Table S5.4). This result suggests that the effects of CD, in combination with SNC, and MFS cannot be explained by the composition of crop types occurring in the mosaic.

Table S5.4. Comparison of estimates for model 1 and model 5 – mosaic crop composition (i.e. model taking into account the composition of crop types in the mosaic). Parameter listed are those retained in the model selection procedure. Parameter estimates and confidence intervals are based on the model averaging approach. ° p<0.1; * p<0.05; ** p<0.01; *** p<0.001.

	model 1	model 5 – mosaic crop composition
Crop diversity (CD)	-0.03 [-2.07 ; 2.01]	-0.06 [-2.1 ; 1.96]
Mean field size (MFS)	-6.39 [-11.85 ; -0.94] *	-6.44 [-11.88 ; -1.01] *
Semi-Natural Cover (SNC)	5.07 [2.87 ; 7.26] ***	5.07 [2.88 ; 7.27 ***
Nb of Crops sampled	2.84 [1.07 ; 4.62] ***	2.84 [1.06 ; 4.62] **

Latitude	1.5 [-3.55 ; 6.55]	1.5 [-3.55 ; 6.55]
Longitude	3.73 [2.47 ; 9.93]	3.73 [-2.47 ; 9.93]
MFS²	3.78 [-0.67 ; 8.23] °	3.73 [-0.72 ; 8.19]
CD :SNC	2.20 [0.64 ; 3.76] **	2.21 [0.65 ; 3.77] **
MFS :SNC	1.15 [-0.66 ; 2.96]	1.15 [-0.66 : 2.96
PCA axis 1		1.5 [-3.55 ; 6.55]

5.5.2. Role of the proportion of grassland in the crop mosaic

The identity of some ecologically important crop types in the mosaic may vary along the gradients of crop diversity and mean field size. In this study, we chose to include managed grassland within agricultural cover types because we were interested in assessing the role of spatial heterogeneity within the farmed part of the landscape. In our dataset, grassland cover was only moderately correlated with crop diversity ($r=-0.001$, $p=0.97$) and mean field size ($r=-0.21$, $p<0.001$). However, we were aware that the proportion of grassland in the crop mosaic, in particular permanent grassland, may have a strong positive effect on biodiversity (Öckinger & Smith 2007).

We added the proportion of grassland to model 1 (using data collected in 435 landscapes from 8 regions) and compared the outcomes of the following model (model 6) with those of model 1.

*Model 6: lmer (T60.landscape ~ CD * MFS * SNC + CD² + MFS² + SNC² + CropNb + Lat + Lon + Grassland + (1| Region/Year))*

Model selection based on model 6 included the same variables as for model 1, plus Grassland, which had a marginally significant positive effect. However, parameter estimates and significance for other variables of interest remained unchanged (Table S5.5). This result suggests that the effects of CD, in combination with SNC, and MFS cannot be explained by the proportion of grassland in the mosaic.

Table S5.5. Comparison of model 1 and model 6 – grassland (i.e. complete model taking into account the proportion of grassland in the mosaic). Parameter listed are those retained in the model selection procedure. Parameter estimates and confidence intervals are based on the model averaging approach. ° p<0.1; * p<0.05; ** p<0.01; *** p<0.001.

	model 1	model 6 – grassland
Crop diversity (CD)	-0.03 [-2.07 ; 2.01]	0.18 [-1.9 ; 2.26]
Mean field size (MFS)	-6.39 [-11.85 ; -0.94] *	-6.2 [-11.83 ; -0.59] *
Semi-Natural Cover (SNC)	5.07 [2.87 ; 7.26] ***	5.07 [2.88 ; 7.27] ***
Nb of Crops sampled	2.84 [1.07 ; 4.62] ***	2.73 [0.94 ; 4.52] **
Latitude	1.5 [-3.55 ; 6.55]	
Longitude	3.73 [2.47 ; 9.93]	4.07 [-2.34 ; 10.47]
MFS²	3.78 [-0.67 ; 8.23] °	3.98 [-0.48 ; 8.44] °
CD :SNC	2.20 [0.64 ; 3.76] **	2.25 [0.69 ; 3.81] **
MFS :SNC	1.15 [-0.66 ; 2.96]	1.33 [-0.51 : 3.16]
Grassland		1.87 [-0.26 ; 4.00] °

5.5.3. Role of semi-natural vegetation occurring between fields

Mean field size (MFS in ha) and the length of semi-natural linear elements between fields (SNL) or the length of hedgerows (H) were strongly correlated, particularly in some regions (e.g. Armorique, Table S5.6). As a result, we could not include both MFS and SNL (or MFS and H) in our models and disentangle their effects on multitrophic diversity.

Table S5.6. Pearson correlation coefficients among explanatory variables across and within regions. CD = crop diversity, MFS = mean field size, SNC= proportion of semi-natural cover, SNL= length of semi-natural linear elements between fields, H = length of hedgerows between fields. N = number of landscapes. Correlations between H and CD or SNC were low and are not shown here for simplicity.

	CD-MFS	CD-SNC	CD-SNL	MFS-SNC	MFS-SNL	MFS-H	SNC-SNL	N
All regions	-0.13	-0.27	-0.30	-0.02	-0.44	-0.37	0.13	435
Armorique	-0.03	0.09	0.10	-0.01	-0.71	-0.67	-0.06	40
Camargue	-0.20	-0.25	0.11	-0.06	-0.55	-0.17	-0.59	40
Coteaux	-0.27	-0.22	0.51	-0.31	-0.57	-0.50	-0.24	32
East Anglia	-0.18	0.21	0.18	-0.16	-0.34	-0.23	-0.41	60
Goettingen	-0.17	0.15	0.05	0.15	-0.43	-0.10	-0.10	52
Lleida	-0.40	-0.14	0.16	-0.15	-0.50	-0.23	-0.20	40
Eastern Ontario	-0.34	-0.13	0.27	-0.40	-0.53	-0.43	-0.08	93
PVDS	-0.16	-0.08	-0.02	-0.37	-0.51	-0.57	0.29	78

To test whether our results for MFS were likely due to the correlation with SNL or H, we selected a subset of landscapes for which explanatory variables, in particular MFS and SNL as well as MFS and H, were uncorrelated i.e. with a Pearson correlation coefficient <0.56 for each pair of explanatory variables, within each region (Table S5.7).

Table S5.7. Pearson correlation coefficients among explanatory variables, across and within regions, within the subset of landscapes (274 landscapes) used to test for the influence of SNL and H on our results for the effects of crop heterogeneity. CD = crop diversity, MFS = mean field size, SNC= proportion of semi-natural cover, SNL= length of semi-natural linear elements between fields, H = length of hedgerows between fields. N = number of landscapes.

	CD-MFS	CD-SNC	CD-SNL	MFS-SNC	MFS-SNL	MFS-H	SNC-SNL	N
All regions	-0.15	-0.30	-0.40	-0.08	-0.27	-0.28	0.30	274
Armorique	-0.02	0.29	0.40	-0.06	-0.04	-0.15	-0.33	20
Camargue	-0.25	-0.19	-0.14	-0.56	-0.05	-0.15	-0.09	20
Coteaux	0.31	-0.38	0.20	-0.46	0.06	-0.12	-0.52	20
East Anglia	-0.15	-0.04	0.35	-0.32	-0.18	-0.31	-0.40	43
Goettingen	-0.26	0.10	0.10	-0.02	-0.22	-0.01	-0.07	45
Lleida	-0.33	0.08	-0.51	-0.37	0.24	-0.20	0.08	20
Eastern Ontario	-0.18	-0.07	-0.03	-0.43	-0.21	-0.32	-0.32	44
PVDS	-0.16	-0.15	-0.08	-0.41	-0.28	-0.46	0.29	62

We built a model similar to model 1 including both SNL and MFS in order to disentangle their effects on multitrophic diversity:

Model 7: $lmer\ (T60.landscape \sim CD * MFS * SNC + CD^2 + MFS^2 + SNC^2 + CropNb + Lat + Lon + SNL + (1| Region/Year))$

Model selection based on model 7 included the same variables as for model 1 (except Latitude and SNC^2), plus SNL. SNL was marginally significant. Parameter estimates and significance for variables of interest remained unchanged (Table S5.8). This results does not confirm the general assumption that the positive effect of MFS is only due to the positive effect of the amount of SNL.

Our variable SNL included a variety of semi-natural linear elements (e.g. hedgerows, grassy margins) that may not play the same role for biodiversity. Therefore, we built another model similar to model 7 including the length of hedgerows (Hedgerow) instead of SNL in order to test whether the effect of MFS on multitrophic diversity may be due to the increase in the length of hedgerows:

*Model 8: lmer (T60.landscape ~ CD * MFS * SNC + CD² + MFS² + SNC² + CropNb + Lat + Lon + Hedgerows + (1| Region/Year))*

Model selection based on model 8 included the same variables as for model 1 (except SNC² and MFS:SNC), plus Hedgerows. Hedgerows were non-significant. Parameter estimates and significance for variables of interest remained unchanged (Table S5.8). This results does not confirm the general assumption that the positive effect of MFS is only due to the positive effect of the amount of SNL or hedgerows. Instead, this result lends support to the idea that agricultural landscapes with smaller fields provide better access to different field types for species that require landscape complementation.

Table S5.8. Comparison of models 1, 7 (with SNL) and 8 (with Hedgerows) based on the uncorrelated subset of landscapes. Parameter listed are those retained in the model selection procedure. Parameter estimates and confidence intervals are based on the model averaging approach. ° p<0.1; * p<0.05; ** p<0.01; *** p<0.001.

	model 1 (subset)	model 7 – SNL	model 8 – Hedgerows
Crop diversity (CD)	-0.14 [-2.9 ; 2.62]	0.39 [-2.39 ; 3.17]	-0.03 [-2.8 ; 2.74]
Mean field size (MFS)	-9.9 [-18.1 ; -1.68] *	-8.92 [-17.24 ; -0.61] *	-8.28 [-16.94 ; 0.38] °
Semi-Natural Cover (SNC)	3.09 ; 0.15 ; 6.03] *	3.16 [0.25 ; 6.07] *	3.17 [0.21 ; 6.14] *
Latitude		2.94 [-3.03 ; 8.9]	
Longitude	2.61 [-2.01 ; 8.89]	2.06 [-4.5 ; 8.62]	2.74 [-4.1 ; 9.58]
MFS²	6.71 [-0.07 ; 13.49] °	6.54 [-0.16 ; 13.24] °	6.33 [-0.44 ; 13.11] °
SNC²		2.71 [0.14 ; 5.34] *	2.6 [-0.03 ; 5.24] °
Nb of Crops sampled	3.87 [1.58 ; 6.17] ***	4.28 [1.98 ; 6.58] ***	3.86 [1.57 ; 6.15] **
CD :SNC	1.85 [-0.28 ; 3.98] °	1.79 [-0.31 ; 3.89] °	1.83 [-0.29 ; 3.96] °
MFS :SNC	0.66 [-2.01 ; 3.32]	0.83 [-1.81 ; 3.47]	
SNL		3.64 [-0.06 ; 7.34] °	
Hedgerows			2.69 [-0.22 ; 5.56] °

5.6 Correlations and alternative mechanisms at the field level

Crop diversity and mean field size are also likely to be correlated with several variables at the field level, including the identity of crops sampled, the local land-use intensity (e.g. herbicide use, ploughing frequency). Disentangling the role of crop heterogeneity from the effects of these other variables is also necessary in order to infer potential mechanisms explaining the positive effect of crop heterogeneity on multitrophic diversity. This required running models at the field level, using a data subset for which co-variable data were available. As a result, we could not include all these variables in a single model and therefore present these analyses as separate, complementary analyses.

5.6.1. Role of the identity of sampled crop types

We tried to limit correlations between the two crop heterogeneity gradients and the identity of sampled crop types. In some cases, correlations were impossible to avoid because some crops occurred or were dominant only in some regions (e.g. rice in Camargue, almond and olive in Lleida) or some landscapes (e.g. landscapes with low crop compositional heterogeneity). As a result, different types of crop sampled were associated with significantly different values of crop diversity or mean field size (Table S5.9).

Table S5.9. Analysis of variance showing the relationship between the two heterogeneity gradients (crop diversity and mean field size) and sampled crop type within each region. Since sampled crop type is a categorical variable, correlation coefficient cannot be used. We therefore used the function aov in R, crop diversity and mean field size being the response variables and sampled crop type being the predictor variable. Values correspond to the F value of the function aov in R. * p<0.05; ** p<0.01; *** p<0.001.

	Crop diversity	Mean field size
All regions	5.78***	9.28***
Armorique	1.95	0.29
Camargue	8.54**	0
Coteaux	1.16	0.59
East Anglia	3.35***	1.29
Goettingen	0	0
Lleida	9.43***	2.18
Eastern Ontario	2.57*	2.61**
PVDS	0.35	0.53

To evaluate whether the sampled crop type influenced our results, we built a model similar to model 1 but using multidiversity calculated at the field level as the response variable (T60.field). We compared models with and without adding crop type as a random effect (using data collected in 1305 fields in 435 landscapes from 8 regions). Crop type was added as a random effect because we were not interested in estimating the specific effect of each particular crop type. Note there were enough crop types (16) to estimate the random effect adequately.

*Model 9: lmer (T60.field ~ CD * MFS * SNC +* CD^2 *+* MFS^2 *+* SNC^2 *+ Lat + Lon + (1| Region/Year/Landscape))*

*Model 10: lmer (T60.field ~ CD * MFS * SNC +* CD^2 *+* MFS^2 *+* SNC^2 *+ Lat + Lon + (1| Region/Year/Landscape) + (1|Crop type))*

To test whether crop type had a significant effect on field-level multitrophic diversity, we used a restricted likelihood-ratio test based on simulated values from the finite sample distribution available in the function exactRLRT from package RLRsim. We then compared the estimates and p-values associated with models 9 and 10 to determine whether any effects of crop type influenced our conclusions regarding the effects of crop heterogeneity on multitrophic diversity.

Although we detected a significant effect of crop type on field-level multitrophic diversity (RLRT = 125.43, p-value < 0.001), adding crop type as a random effect in the model did not change the outcome of model selection or the significance of variables of interest (Table S5.8). This result suggests that variations in the identity of crops sampled do not explain the effects of CD, in combination with SNC, and MFS on multitrophic diversity detected in our study.

Table S5.10. Comparison of models built at the field level for multitrophic diversity (model 9 – field level, i.e. without sampled crop type as a random effect; model 10 – sampled crop id, i.e. with sampled crop type as a random effect). Parameter listed are those retained in the model selection procedure. Parameter estimates and confidence intervals are based on the model averaging approach. ° p<0.1; * p<0.05; ** p<0.01; *** p<0.001.

	model 9 (field)	model 10 (field) – sampled crop ID
Crop diversity (CD)	0.78 [-0.79 ; 2.36]	0.25 [-2.08 ; 2.58]
Mean field size (MFS)	-3.14 [-6.57 ; 0.28] °	-2.44 [-4.77 ; -0.10] *
Semi-Natural Cover (SNC)	3.14 [-1.12 ; 7.4]	3.79 [0.98 ; 6.60] **
Latitude	0.97 [-3.4 ; 5.33]	
Longitude	3.63 [-1.68 ; 8.93]	1.2 [-4.88 ; 7.28]
CD²		0.67 [-4.25 ; 5.6]
MFS²	2.07 [-1.52 ; 5.66]	1.19 [-2.38 ; 4.76]
SNC²	2.9 [-1.27 ; 7.06]	2.05 [-2.08 ; 6.18]
CD :SNC	1.35 [0.08 ; 2.63] *	1.39 [0.14 ; 2.63] *
MFS :SNC	1.55 [0.09 ; 3.00] *	1.91 [0.47 ; 3.34] **
CD :MFS		0.2 [-1.12 ; 5.56]

5.6.2. Role of crop heterogeneity in cereal fields

To further assess the role of crop identity, we applied model 9 to the subset of data collected in cereal fields. Indeed, cereal is the most widespread crop type sampled in our dataset and the only one present in all regions. We therefore applied model 6 on 615 fields in 334 landscapes in our 8 regions (after removing the random effect of landscape since most landscape contain only one cereal field). This analysis confirms that decreasing MFS and, when SNC is high enough, increasing CD have positive effects on multitrophic diversity in cereal crop fields (Table S5.11).

Table S5.11. Comparison of models built at the field level for multitrophic diversity (model 9) with the complete dataset and with the cereal subset. Parameter listed are those retained in the model selection procedure. Parameter estimates and confidence intervals are based on the model averaging approach. ° p<0.1; * p<0.05; ** p<0.01; *** p<0.001.

	model 9 (field) – complete dataset	model 9 (field) – cereal subset
Crop diversity (CD)	0.78 [-0.79 ; 2.36]	-2.78 [-8.62 ; 3.06]
Mean field size (MFS)	-3.14 [-6.57 ; 0.28] °	-4.51 [-9.24 ; 0.23] °
Semi-Natural Cover (SNC)	3.14 [-1.12 ; 7.4]	3.16 [0.26 ; 6.06] *
Latitude	0.97 [-3.4 ; 5.33]	
Longitude	3.63 [-1.68 ; 8.93]	2.03 [-0.87 ; 4.94]
MFS²	2.07 [-1.52 ; 5.66]	3.62 [-0.19 ; 7.43] °
SNC²	2.9 [-1.27 ; 7.06]	1.49 [-3.09 ; 6.08]
CD :SNC	1.35 [0.08 ; 2.63] *	1.76 [0.17 ; 3.36] *
MFS :SNC	1.55 [0.09 ; 3.00] *	3.31 [1.73 ; 4.9] ***
CD :MFS		0.46 [-1.17 ; 2.09]

5.6.3. Role of field-level Land-Use Intensity

Land-use intensity may be correlated with crop heterogeneity in some regions. For instance, landscapes with larger mean field sizes may be associated with higher fertilizer inputs (Levers et al. 2016, Roschewitz et al. 2005). Such correlations could hamper our ability to draw conclusion on the effects of crop heterogeneity on multitrophic diversity.

We conducted farmer surveys to collect data on land use intensity of the sampled fields. Information included ploughing (0=no/1=yes), use of fertilizer (0=no/1=yes), frequency of herbicide use (from 0 to 7) and frequency of insecticide use (from 0 to 6) in 324 fields located in 132 landscapes across five regions (Armorique, Camargue, Coteaux, Goettingen and Eastern Ontario). We calculated a local Land-Use Intensity index (local LUI) based on the normalized mean of these four variables (after scaling each variable) following a formula similar to the one developed by Herzog et al. (2006): LUI = ¼ (scale(ploughing) + scale(fertilizer) + scale(herbicide) + scale(insecticide)). This local LUI index therefore varies between 0 (low intensity) and 1 (high intensity).

The Pearson correlation between local LUI and crop diversity was weak and not significant (r=0.10; p=0.12). The Pearson correlation between local LUI and mean field size was negative (i.e. opposite to expectation; r= -0.27; p<0.001; Fig. S5.4).

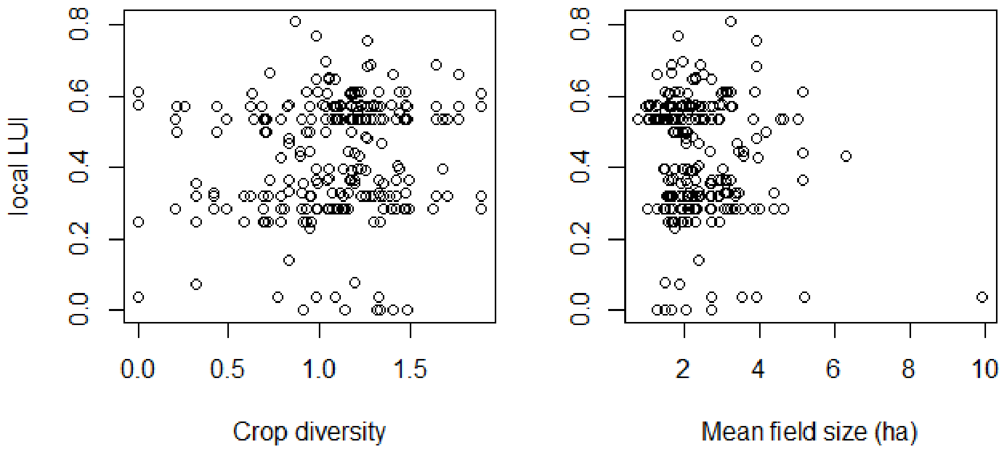


Figure S5.4. Relationship between the two crop heterogeneity gradients and Land-Use Intensity (LUI).

We added local LUI to model 10 and compared the outcomes of model 10 and model 11 using the data subset for which Field LUI data was available.

*Model 11: lmer (T60.field ~ CD * MFS * SNC +* $CD^2 + MFS^2 + SNC^2$ *+ Lat + Lon + Field LUI + (1|Region/Year/Landscape) + (1|Crop type))*

Model selection based on model 11 included almost the same variables as for model 10, plus Field LUI, which had a significant negative effect. Parameter estimates for model 10 using the LUI data subset differ slightly from parameter estimates due to the fact that more complex interactions were included. However, we checked that the overall shape of the relationships do not differ much between the model based on the whole dataset and the model based on the LUI dataset. More importantly, parameter estimates and significance for other variables of interest remained very similar between model 10 and model 11 (Table S5.12). This result suggests that the effects of mean field size and crop diversity cannot be explained by variations in field-level land-use intensity. It is interesting to note that we observe here a significant negative interaction between crop diversity and mean field size which is consistent with the 'landscape complementation' hypothesis, i.e. the fact that multitrophic diversity benefit more from increasing crop diversity when fields become smaller and can be reached more easily. However, the fact that this relationship was not observed in other models calls for further investigations.

Table S5.12. Comparison of models built at the field level for multitrophic diversity with and without field-level land use intensity (LUI). Parameter listed are those retained in the model selection procedure. Parameter estimates and confidence intervals are based on the model averaging approach. ° p<0.1; * p<0.05; ** p<0.01; *** p<0.001.

	model 10 (field level LUI subset)	model 11 (field level LUI subset) - LUI
Crop diversity (CD)	18.1 [5.35 ; 20.85] **	16.14 [3.42 ; 28.86] *
Mean field size (MFS)	8.81 [0.31 ; 17.31] *	8.32 [-0.41 ; 17.05] °

Semi-Natural Cover (SNC)	17.69 [6.26 ; 29.12] **	19.11 [7.9 ; 30.33] ***
Latitude	4.38 [0.95 ; 7.82] *	5.91 [1.72 ; 10.09] **
Longitude	2.98 [-0.19 ; 6.15] °	
CD^2	-15.54 [-27.25 ; -3.83] **	-14.25 [-25.88 ; -2.61] *
MFS^2	-12.27 [-21.8 ; -2.7] *	-13.33 [-22.78 ; -3.88] **
SNC^2	-15.76 [-27.97 ; -3.54] *	-17.9 [-29.89 ; -5.91] **
CD :SNC	-4.8 [-8.53 ; -1.06] *	-5.2 [-8.86 ; -1.55] **
MFS :SNC	2.55 [-0.77 ; 5.86]	
CD :MFS	-4.06 [-7.55 ; -0.57] *	-3.8 [-6.71 ; -0.87] *
CD :MFS :SNC	1.6 [-0.99 ; 4.19]	
Field LUI		-2.53 [-4.79 ; -0.26] *

5.7. Moving window modeling approach for Crop heterogeneity × Semi-natural cover interaction

We used a moving window modeling approach (Humpries et al. 2010; Berdugo et al. 2018) to identify potential discontinuities in the response of multitrophic diversity measured at the landscape level (T60.landscape) to crop diversity and mean field size along the gradient of semi-natural cover. To do so, we ordered all landscapes (n = 435) along the gradient of semi-natural cover (%) and selected the first 75 landscapes with the lowest semi-natural cover. Using this subset, we ran the model obtained from the averaging approach applied to model 1 (Fig. 2A main text) after excluding semi natural cover and its interactions with CD and MFS, such as:

*Model 12: lmer (T60.landscape ~ CD*MFS + MFS² + CropNb + Lat + Lon + (1| Region/Year))*

We then extracted and stored the model coefficient for crop diversity (CD), mean field size (MFS) and the confidence intervals (CIs). We then removed the landscape with the lowest value of semi-natural cover from the subset of 75 landscapes, added the landscape scoring the next higher value, ran model 12 and extracted model coefficients and CIs. We repeated this loop as many times as landscapes remained along the entire gradient of semi-natural cover (n = 286 subsets, see R code below). We saved all coefficients and confident intervals for each step and plotted them against the gradient of semi-natural cover (Fig. S5.5).

Consistently with our multiple regression analyses (Fig. 2A in main text), this moving window analysis showed that the effect of crop diversity and mean field size on multitrophic diversity changes along the gradient of semi-natural cover (Fig. S5.5 A and B). The effect of crop diversity is positive for high values of semi-natural cover, neutral as semi-natural cover decreases and negative for the low values of semi-natural cover. The effect of mean field size is neutral for the high values of semi-natural cover and negative for low values of semi-natural cover.

However, this analysis reveals that changes in the effect of crop diversity and mean field size on multitrophic diversity are not smooth but instead show abrupt transitions when semi-natural cover decreases. For crop diversity, there is an abrupt change at 11.2% of semi-natural cover where the effect of crop diversity shifts abruptly from positive to neutral and one at 4.5% where the effect of crop diversity shifts from neutral to negative. For mean field size, there is one abrupt change at 8% where the effect of mean field size shifts abruptly from neutral to negative. This analysis allows identifying three thresholds that can be used to guide recommendations on how to manage the three main components of agricultural landscape heterogeneity, namely crop diversity, mean field size and the amount of semi-natural cover (see main text for more details).

R Code for the Moving Window Analysis (the code provided only concerns crop diversity)

```
##### moving window function
WindowSKR <- function(df,Factor,X,Y,formul,n=10){
  myvars<-c(Factor,X,Y)
  dftemp = df[myvars]
  dftemp = dftemp[order(dftemp[Factor]),]
  tt=length(unlist(dftemp[Factor]))-n
  i = 1
  mdl <- lmer(data = dftemp, formula = formul)
  res<- matrix(data = NA,nrow = 1,ncol = length(fixef(mdl))+1)
  ci<-res
  library(lme4)
  while(tt>n){
    dfi <- dftemp[i:(i+n),]
    Fact <- mean(unlist(dfi[Factor]))
    mdl <- lmer(data = dfi, formula = formul, na.action = na.fail,REML ="TRUE")
    #dist<- mean(unlist(dfi[X]))+1-mean(unlist(dfi[Y]))
    res <- rbind(res,c(Fact,fixef(mdl)))
    cii <- (abs(confint(mdl)[-c(1,2),1]-confint(mdl)[-c(1,2),2]))/2
    ci<-rbind(ci,c(Fact,cii))
    tt=tt-1
    i=i+1
  }
  res<- as.data.frame(res)
  ci<-as.data.frame(ci)
  colnames(res)<-c("MWfactor",names(fixef(mdl)))
  colnames(ci)<-c("MWfactor",names(fixef(mdl)))
  RES<-list(res=res,ci=ci)
  return(RES)
}

##### uploading libraries
library(jsonlite)
library(ggplot2)
library(tidyr)
library(boot)
library(lme4)

#### running moving window analysis
formul<-T60.landscape~ Crop_SHDI+Crop_MFS  +  sampled.crop.nb + MFS2 + Lon + Lat +  (1|Region/Year) -1
RES <- WindowSKR(df,"Seminat_Cover",c("Crop_SHDI","MFS2","Crop_MFS", "Seminat_Cover",
"sampled.crop.nb", "Region",  "Year",  "Lon",  "Lat"),"T60.landscape",formul,n=75)

#### plotting results of the moving window analysis
dfres=data.frame(MWfactor<-RES$res$MWfactor, Effect<-RES$res$Crop_SHDI, CI<-RES$ci$Crop_SHDI)
limits <- aes(ymax = Effect + CI, ymin=Effect - CI)
p1<-ggplot(data = dfres,aes(x = MWfactor,y = Effect), ylim = c(1,4))+
  geom_line(col = "olivedrab3")+
  geom_point(col = "olivedrab3")+
  geom_pointrange(limits,col = "olivedrab3")+
  xlab("Semi-Natural Cover (%)")+
```

```
  ylab("Effect of Crop Diversity")
p1 + theme(axis.text=element_text(size=14), axis.title.x = element_text(size=18, face="bold"), axis.title.y =
element_text(size=18, face="bold"))
```

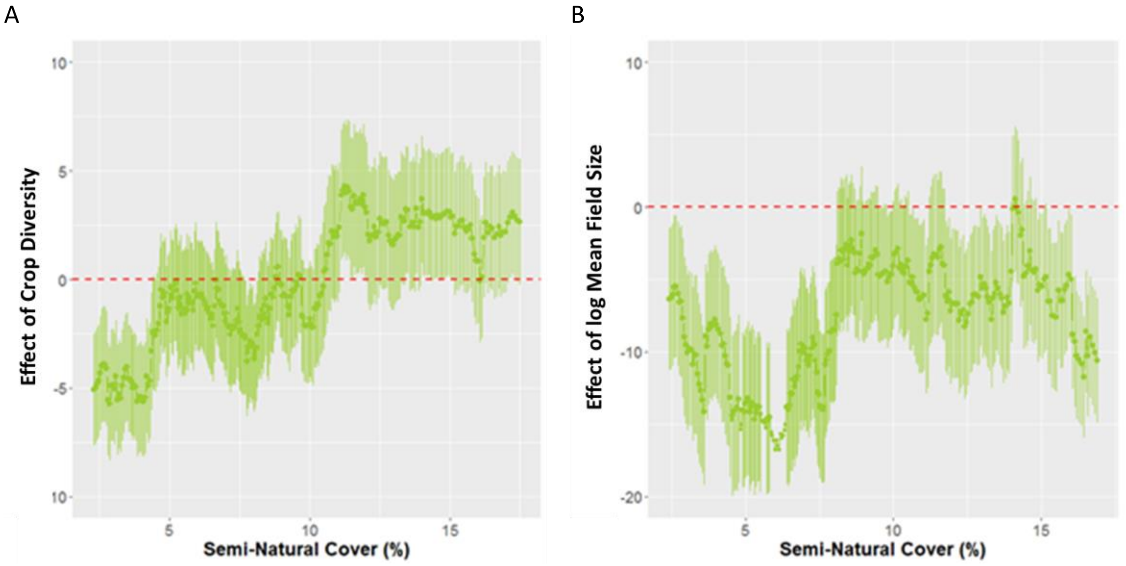


Figure S5.5. Effect of crop diversity (A) and mean field size (B) on multitrophic diversity for different levels of semi-natural cover. Parameter estimates and confidence intervals are based on a moving window analysis (see detailed description in SI5). The red line indicates a null effect. Each dot and CI correspond to the estimate values of CD or MFS for the average semi-natural cover of a given window along the semi-natural cover gradient. Due to the low number of landscapes with semi-natural cover >17.5% (Table S4.1), we only represent the gradient between 0 and 17.5% of semi-natural cover on these figures.

References

Berdugo M, et al. Aridity preferences alter the relative importance of abiotic and biotic drivers on plant species abundance in global drylands. J Ecol 0(0). doi:10.1111/1365-2745.13006.

Herzog F, et al. (2006) Assessing the intensity of temperate European agriculture at the landscape scale. Eur J Agron 24(2):165–181.

Humphries NE, et al. (2010) Environmental context explains Lévy and Brownian movement patterns of marine predators. Nature 465(7301):1066–1069.

Levers C, Butsic V, Verburg PH, Müller D, Kuemmerle T (2016) Drivers of changes in agricultural intensity in Europe. Land Use Policy 58(Supplement C):380–393.

Öckinger E & Smith HG (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. Journal of applied ecology 44(1): 50-59.

Roschewitz I, Thies C, Tscharntke T (2005) Are landscape complexity and farm specialisation related to land-use intensity of annual crop fields? Agric Ecosyst Environ 105(1–2):87–99.