



# Ecological performance underlying ecosystem multifunctionality is promoted by organic farming and hedgerows at the local scale but not at the landscape scale

Eloïse Couthouis, Stéphanie Aviron, Julien Pétillon, Audrey Alignier

## ► To cite this version:

Eloïse Couthouis, Stéphanie Aviron, Julien Pétillon, Audrey Alignier. Ecological performance underlying ecosystem multifunctionality is promoted by organic farming and hedgerows at the local scale but not at the landscape scale. *Journal of Applied Ecology*, 2023, 60 (1), pp.17-28. 10.1111/1365-2664.14285 . hal-03923082

**HAL Id: hal-03923082**

**<https://hal.science/hal-03923082>**

Submitted on 15 Feb 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

**Ecological performance underlying ecosystem multifunctionality is promoted by organic farming and hedgerows at the local scale but not at the landscape scale**

Couthouis E.<sup>a,b</sup>, Aviron S.<sup>a</sup>, Pétillon J.<sup>b,c</sup>, Alignier A.<sup>a,d</sup>

<sup>a</sup> UMR BAGAP, INRAE – L’Institut Agro Rennes-Angers – ESA Angers, 35042 Rennes, France

<sup>b</sup> UMR ECOBIO, CNRS – Université de Rennes 1, 35042 Rennes, France

<sup>c</sup> Institute for Coastal and Marine Research, Nelson Mandela University, 6031 Port Elizabeth, South Africa

<sup>d</sup> LTSER Zone Atelier Armorique, 35042 Rennes, France

**Corresponding author:**

Audrey Alignier, [audrey.alignier@inrae.fr](mailto:audrey.alignier@inrae.fr), +33 (0)2 23 48 57 70

**Manuscript word count (excluding supporting information): 8964**

## Abstract

1. The relative contributions of agricultural intensity and semi-natural habitats to the multifunctionality and sustainability of ecosystems at different spatial scales remain largely under-investigated.
2. In this study, we assessed the multifunctionality of 40 winter cereal fields and 40 hedgerows based on ecological, agronomic and socio-economic performance using data from field surveys and interviews with farmers. We specifically focused on the effects of local farming systems (organic vs. conventional) and management (cereals intercropped with legumes vs. monocrops), the effects of landscape heterogeneity related to hedgerow density, and the spatial extent of semi-natural habitat and organic farming.
3. Multifunctionality indices associated with increased values of proxies for biodiversity conservation and pest control functions were higher for hedgerows than crop fields.
4. Agroecosystem multifunctionality was similar between organic and conventional farming as a consequence of antagonistic responses of individual function proxies. While organic farming promoted ecological performances of crops, conventional farming resulted in higher agronomic performances (i.e. yield). Interestingly, lower yields of organic crops were not systematically associated with reductions in socio-economic performance in terms of farmer income and labour.
5. At the landscape scale, hedgerow density and the extent of semi-natural habitats and organic farming had little influence on agroecosystem multifunctionality or individual function proxies.
6. *Synthesis and applications.* Our results confirm the high value of hedgerows and organic farming at the local scale for the ecological performance of ecosystems. Our study suggests that, among existing agri-environment schemes in Europe, hedgerow planting

and organic farming are appropriate tools to optimise the ecological performance of ecosystems at the local scale even if antagonistic effects with agronomic performance should not be neglected.

**Keywords:** Above-ground biodiversity, hedgerows, landscape, organic farming, pollination, pest control, socio-economic performance, yield

## Résumé (French)

1. Les contributions relatives de l'intensité de l'agriculture et des habitats semi-naturels à la multifonctionnalité et à la durabilité des écosystèmes à différentes échelles spatiales restent largement sous-étudiées.

2. Dans cette étude, nous avons évalué la multifonctionnalité de 40 parcelles de céréales d'hiver et de 40 haies sur la base de leurs performances écologiques, agronomiques et socio-économiques, en utilisant des données provenant à la fois de relevés de terrain et d'entretiens avec des agriculteurs. Nous nous sommes spécifiquement concentrés sur les effets des systèmes agricoles locaux (biologiques ou conventionnels) et de la gestion (céréales en association avec des légumineuses ou monocultures), et les effets de l'hétérogénéité du paysage liée à la densité des haies, à l'étendue spatiale des habitats semi-naturels et à l'étendue des surfaces en agriculture biologique.

3. La multifonctionnalité, associée à des valeurs accrues d'indicateurs de conservation de la biodiversité et de lutte contre les ravageurs des cultures, était plus élevée pour les haies que pour les cultures.

4. La multifonctionnalité des parcelles cultivées ne variait pas entre agriculture conventionnelle et agriculture biologique, du fait de réponses antagonistes entre fonctions. Alors que l'agriculture biologique favorise les performances écologiques, l'agriculture conventionnelle est associée à des performances agronomiques plus élevées (i.e. le rendement). Il est intéressant de noter que les rendements inférieurs des parcelles en agriculture biologique n'étaient pas systématiquement associés à des réductions des performances socio-économiques en termes de revenu et de travail des agriculteurs.

71 5. À l'échelle du paysage, la densité des haies, l'étendue spatiale des habitats semi-  
72 naturels et l'étendue spatiale de l'agriculture biologique avaient peu d'influence sur la  
73 multifonctionnalité des parcelles ou sur les indicateurs de fonctions considérées  
74 individuellement.

75 6. Synthèse et applications. Nos résultats confirment la grande valeur des haies et  
76 de l'agriculture biologique à l'échelle locale pour les performances écologiques des  
77 écosystèmes. Notre étude suggère que, parmi les programmes agri-environnementaux  
78 existants en Europe, la plantation de haies et l'agriculture biologique sont des outils  
79 appropriés pour optimiser les performances écologiques des écosystèmes à l'échelle  
80 locale même si des effets antagonistes avec les performances agronomiques existent et  
81 ne doivent pas être négligés.

## 1. Introduction

Faced with global climate change and biodiversity crises, there is an urgent need to shift from intensively managed landscapes toward landscapes comprising multifunctional ecosystems that simultaneously provide multiple functions to support the goods and services needed by society (Stürck & Verburg, 2017). Enhancing ecosystem multifunctionality in agricultural landscapes presents significant challenges, given that it requires both a holistic view and practical tools to reconcile the needs of agricultural production, biodiversity conservation, and ecosystem functioning (Manning et al., 2018; Hölting et al., 2019).

In agricultural landscapes, ecosystem multifunctionality is generally investigated with a focus on agroecosystems, based on consideration of their ecological, socio-economic and agronomic performance. Whereas agronomic performance is largely centred on food production, socio-economic performance takes into account the income and well-being of farmers (Wittwer et al., 2021). With respect to ecological performance, it is accepted that agroecosystems benefit from the multiple functions carried by biodiversity, including natural pest control and pollination (Dainese et al., 2019). Conversely, there is growing interest in the potential contribution of agriculture to biodiversity conservation (Tilman et al., 2014), even where biodiversity may also be associated with negative externalities such as pest infestation of crop fields (Zhang et al., 2007).

Gaining an understanding of the multiple drivers of ecosystem multifunctionality clearly necessitates a consideration of different spatial scales (Wu & David, 2002). At the field or farm scale, organic farming (OF) is considered a promising system for promoting multifunctionality (Shennan et al., 2017; Smith et al., 2020; Wittwer et al., 2021). Many studies have revealed that compared with conventional farming (CF), OF is beneficial for preserving farmland biodiversity, including pollinator and predator communities (Tuck et al., 2014; Lichtenberg et al., 2017). Although OF systems are often characterised by lower agronomic performance (i.e.,

crop productivity) (Shennan et al., 2017), they can be particularly profitable for farmers in terms of income (underpinned by subsidies) and quality of life (Shennan et al., 2017; Smith et al., 2020). However, if current organic subsidies are reduced or no longer applied, the economic benefits of OF could be lower than those of CF (Crowder and Reganold, 2015). Alongside OF, the conservation or implementation of semi-natural elements adjacent to crop fields, such as hedgerows, provide another way to promote local biodiversity (Dainese et al., 2017; Baudry et al., 2000) and associated ecosystem services such as natural pest control and pollination (Montgomery et al., 2020). Indeed, hedgerows may act as a refuge and provide habitats and overwintering sites for above-ground biodiversity (Sarhou et al., 2014; Garratt et al., 2017). Hedgerows are thus thought to be more multifunctional than cultivated fields (Van Vooren et al., 2018), despite potential negative externalities for agroecosystems, including the provision of shelter for crop pests (Fusser et al., 2016).

Beside local drivers, there is growing evidence that a landscape perspective is essential for promoting multifunctionality (Dainese et al., 2017; Botzas-Coluni et al., 2021). In this regard, landscape heterogeneity, defined as the composition (i.e. diversity and amount) and configuration (i.e. spatial arrangement) of landscape elements (Fahrig et al., 2011) is assumed to play a key role for biodiversity and ecological processes (Benton et al., 2003; Tschardt et al., 2012). Among studies investigating the effects of landscape heterogeneity on multifunctionality, most have focused on few ecological functions, generally studied one-by-one (Holzschuh et al., 2008; Chaplin-Kramer et al., 2011). Studies focusing on multi-diversity (Sirami et al., 2019) or on simultaneous ecological and agronomic performance (Martin et al., 2016; Martin et al., 2019; Smith et al. 2020; Botzas-Coluni et al., 2021) are particularly scarce. These studies revealed that a large amount of semi-natural habitat (SNH) and application of OF methods are beneficial for pollinators and natural pest enemies. They also showed that increasing landscape configuration (by decreasing mean field size or increasing edge density)



benefited multitrophic diversity (Sirami et al. 2019) as well as pollination and pest regulation (Martin et al., 2019; Botzas-Coluni et al., 2021). Conflicting results about the effect of landscape configuration on agronomic performance (mainly crop yield) have been reported; increasing mean field size benefited crop yield (Botzas-Coluni et al., 2021), and arable-dominated landscapes with high edge densities achieved high yields (Martin et al., 2016; Martin et al., 2019). Smith et al. (2020) showed that yield gaps between organic and conventional farms increased and profitability benefits of OF decreased as crop field size increased in the landscape. Despite these studies, there remains relatively little information available regarding the influence of landscape heterogeneity on agroecosystem multifunctionality.

In the present study, we investigated the effects of OF and hedgerows on the multifunctionality of ecosystems in agricultural landscapes at different spatial scales. Specifically, we focused on (i) ecological performance associated with above-ground biodiversity (conservation, pollination, pest control and pest infestation), (ii) socio-economic performance (income and indicators of farmer labour), and (iii) agronomic performance (yield). At the local scale, we expected higher multifunctionality correlated with ecological performance in hedgerows than in crop fields. We also expected agroecosystem multifunctionality to be higher in OF fields compared with CF fields. Lastly, we expected higher agroecosystem multifunctionality in heterogeneous landscapes (i.e. those with a higher proportion of SNH and OF and/or higher hedgerow density).

## **2. Materials and methods**

### **2.1. Study site**

The study was conducted in the Zone Atelier Armorique (47°55'N, 1°38'W), north-western France (European LTER Network; [osur.univ-rennes1.fr/za-armorique/](https://osur.univ-rennes1.fr/za-armorique/)). This area is characterised by a dense hedgerow network (bocage), mixed dairy farming and cereal

production. The cultivated area is dominated by winter cereals and maize, along with grassland, and is interspersed with semi-natural elements (i.e. woodlots and hedgerows).

We selected 40 winter cereal fields (20 fields under OF and 20 under CF), distributed along two independent landscape gradients (Spearman correlation,  $\rho = 0.19$ ) based on (i) the varying extent (percentage cover) of OF (from 0% to 82% in 500 m radius circles centred on studied fields), and (ii) the varying density (length) of hedgerows (from 1368 m to 5953 m, in 500 m radius circles; Fig. 1). The average distance between selected fields was  $1361.12 \pm 253.32$  m and the minimum distance was 222.10 m. Cereal fields were under monoculture of winter cereals such as wheat (*Triticum* spp.), triticale (*Triticosecale* spp.) or oat (*Avena sativa* L.), hereafter referred to as ‘Cereal crops’ (10 OF and 20 CF fields), or winter cereals intercropped with legumes, namely faba bean (*Vicia faba* L.) or pea (*Pisum sativum* L.), without distinct row arrangement, hereafter referred to as ‘Mixed crops’ (10 OF fields; see Table S1 in Supporting Information). This design reflects the practices of farmers in the study area, namely frequent cultivation of ‘Mixed crops’ on OF farms, and a predominance of ‘Cereal crops’ on CF farms. Field size was comparable between CF, OF Cereal crops and OF Mixed crops. In addition, there were no significant differences in management practices (number of interventions, fertiliser input and ploughing) between OF Cereal crops and OF Mixed crops (Fig. S1). Surveys were conducted both in the centre of focal fields and in their adjacent hedgerows. Hedgerows were all characterised by the simultaneous presence of herbaceous, shrub, and tree layers. All farmers gave us permission for fieldwork. The study did not require ethical approval.

## 2.2. Ecological, agronomic, and socio-economic performance

Multifunctionality was assessed based on (i) four ecological functions (biodiversity conservation, pollination, pest control and pest infestation) based upon abundance or richness of taxa as proxies of ecological performance; (ii) two functions (labour and semi-net margin)

as proxies of socio-economic performance; and (iii) one function (crop yield) as a proxy of agronomic performance (Fig. 1).

### 2.2.1 Proxies of ecological functions

To assess ecological functions, we conducted field sampling of predatory arthropods, insect pests, flower-visiting insects and spontaneous vegetation. Predatory arthropods (carabids; *Coleoptera: Carabidae*), spiders (*Araneae*), staphylinids (*Coleoptera: Staphylinidae*), ladybirds (*Coleoptera: Coccinellidae*) and insect pests (aphids; *Hemiptera: Aphidoidea*) were collected twice, in May and June 2020, using a vacuum method (D-vac), with a series of five aspirations performed at 10-m intervals along a 50 m-long transect located in each habitat (hedgerow and centre of the field; see details in Appendix S1). The D-vac aspirations were carried out through the vegetation and on the ground in order to capture the arthropods present on these two strata. Data from the series of aspirations (N = 5) and the sampling periods (N = 2) were pooled to obtain estimates of the total abundance of predatory arthropods and aphids per habitat type (hedgerow or crop field). Carabid beetles were identified at the species level following Roger et al. (2010). Visual counts of flower-visiting insects were performed three times in May, June and July 2020, by walking along 50 m-long transects (one per habitat) at a slow pace for 5 min. Flower-visiting insects were assigned to one of the following morphogroups: honeybees, *Bombus terrestris* agg., *Bombus lapidarius*, *Bombus pascuorum*, solitary bees < 1 cm, solitary bees > 1 cm, aphidophagous hoverflies, non-aphidophagous hoverflies, butterflies, other Diptera, other Coleoptera and other Hymenoptera. Data were pooled over the three sampling periods to determine the abundance and richness of morphogroups of flower-visiting insects per habitat. Single surveys of spontaneous vegetation were conducted in 10 quadrats (1 × 1 m) placed at 5 m intervals along each 50 m-long transect. Plant species were identified according to *Flora Europaea* (Tutin et al., 1993) and corresponding percentage cover was estimated visually. We distinguished troublesome weeds (i.e. species that potentially cause

high yield losses or hinder harvesting operations) based on expert knowledge from personnel at the Chamber of Agriculture of Brittany, France).

From this dataset, we estimated the biodiversity conservation function by simultaneously considering the total species richness of carabid beetles, vascular plants, and the number of morpho-groups of flower-visiting insects. The abundance of flower-visiting insects was used as a proxy of the pollination function whereas the abundance of all predatory arthropods was used as a proxy of the pest control function. Aphid abundance and the mean cover of troublesome weeds were selected as proxies of the pest infestation function.

### ***2.2.2 Proxies of agronomic and socio-economic functions***

We conducted interviews with farmers (OF fields = 16 farmers; CF fields = 17 farmers) to obtain data on soil preparation practices (from harvest of the preceding crop [ $n - 1$ ] to sowing of the next crop [ $n + 1$ ]), pest management (mechanical or chemical weeding, fungicide, insecticide and molluscicide use), fertilisation (mineral or organic), and harvested products (yield). In a few cases, two to three fields were managed by the same farmer. Regardless, data collected were specific to each field (i.e. farmers who managed more than one field provided information for each field). We used Agrosyst software (Jolys et al., 2016) to calculate socio-economic performance (i.e. labour and semi-net margin). The labour proxy ( $\text{h.ha}^{-1}$ ) corresponded to the cumulative duration of interventions in sampled fields, while the semi-net margin ( $\text{€}.\text{ha}^{-1}$ ) was calculated by subtracting operational expenses (seeds and inputs) and equipment (depreciation, maintenance and gasoline) from the market price of crops. The semi-net margin closely approximates the actual income of farmers.

## **2.3. Multifunctionality indices**

Various methods exist for synthesising the multifunctionality of ecosystems that attribute different weight to the importance of individual functions and services. A straightforward and

common technique consists of summing or averaging all functions and services in a considered ecosystem. Alternatively, the ‘threshold approach’ accounts for functions and services that are above a certain threshold, based on the assumption that only high supply levels contribute a value to the multifunctional environment (Byrnes et al. 2014; Hölting et al. 2019). Here, we used the ‘averaging approach’, by averaging the normalised values of proxies to yield a single index. The two main methods for normalization are standardisation by the maximum value (Mouillot et al. 2011) or using z-score (Maestre et al. 2012). Here, we standardised each function using the maximum observed value across all sites to remove the effects of differences in the scales of measurement among functions. In the case of functions for which negative values indicate higher levels of function (i.e. infestation and labour), the values of the proxies were inverted such as 1-infestation and 1-labour. Although there are certain reservations regarding the use of maximum values for standardisation (e.g. sensitivity to outliers), standardising the scale of a multifunctional index by a maximum value creates a metric that is intuitively understandable in comparison with the z-score method (Manning et al., 2018). We also applied normalisation using the z-score method (by subtracting the mean of the values and dividing by the standard deviation) to compare the sensitivity of our results in relation to the standardisation method. In that latter case, we transformed labour and infestation to a negative scale by multiplying by -1. Differences in results between the two methods were highlighted.

#### **2.4. Landscape variables**

Land-cover maps of the landscape sites were digitised using aerial ortho-photographs (BD ORTHO IGN, 2017) and field surveys using Arcgis 10.8.1 (Environmental Systems Resource Institute; ESRI, 2020). Nine land-cover types (woodland, hedgerows, grassland, herbaceous strips, winter cereal, maize, other crop, water, and urban area) were mapped in 1000 m radius circles centred on each sampled field. In addition, maps of farming systems (OF vs. CF) were

created based on existing data obtained for the same study area (Puech et al., 2015) and updated based on information obtained from our interviews with farmers in the present study.

From these maps, we calculated two metrics for landscape composition (the percentage cover of SNH [% SNH including woodlands, permanent grasslands, hedgerows and fallows] and the percentage cover of OF (without the focal OF fields [% OF]); and one metric for landscape configuration: (hedgerow density [total hedgerow length]; Fig. S2). All metrics were calculated in 250 m, 500 m and 1000 m radius circles using Chloe software (Boussard et al., 2020). According to Dormann et al. (2013), we considered data not overly correlated when Spearman  $\rho < |0.7|$ . We detected no strong correlation between landscape metrics (Table S2).

## 2.5. Statistical analysis

First, we compared the multifunctionality of hedgerows and crop fields. We generated a ‘biodiversity-related’ multifunctionality index based upon the four proxies describing ecological performance. We used generalized linear mixed models (GLMMs) with habitat type (hedgerow vs. crop field) as a fixed effect and the identity of the field (Field ID) as a random effect to account for the spatial non-independence between fields and hedgerows. The model formula was:

$$[1] \quad X \sim \text{Habitat type (hedgerow vs. crop field)} + (1 | \text{Field ID})$$

where X is the biodiversity-related multifunctionality index or associated proxies of ecological functions.

Second, we tested the effect of agricultural management (CF, OF Cereal crops and OF Mixed crops) on the multifunctionality index and proxies of ecological, agronomic and socio-economic functions using generalized linear models (GLMs). We generated a second (agroecosystem) multifunctionality index, dedicated to crop fields, integrating the seven

proxies describing ecological, agronomic and socio-economic performances. The model formula was:

$$[2] \quad Y \sim \text{Agricultural management (CF vs. OF}_{\text{cereal crops}} \text{ vs. OF}_{\text{mixed crops}})$$

where Y is the agroecosystem multifunctionality index or associated proxies of functions.

Lastly, GLMs were used to assess the effects of local farming system (OF vs. CF) and landscape heterogeneity (% SNH, % OF and hedgerow density) on the agroecosystem multifunctionality index and associated proxies of functions at 250 m, 500 m and 1000 m, according to the formula:

$$[3] \quad Y \sim \text{Farming system (CF vs. OF)} + \% \text{ SNH} + \% \text{ OF} + \text{hedgerow density}$$

According to standardisation by the maximum value, multifunctionality index and proxy values ranged from 0 to 1. We thus used the Beta family in GLMMs (model [1]) with the ‘glmmTMB’ R package (Brooks et al., 2020) and a Beta distribution in GLMs (models [2] and [3]) using the ‘betareg’ R package (Zeileis et al., 2021). According to standardisation by z-score, multifunctionality index and proxy values followed a normal distribution. Explanatory variables were centred and scaled to enhance the interpretability and comparison of regression coefficients (Schielzeth, 2010). For model [3], a full averaging procedure of models was performed with a  $\Delta\text{AICc}$  value  $<4$  (Burnham et al., 2011) using the MuMIn R package (Bartoń, 2020). We checked for multi-collinearity (Cade, 2015) using variance inflation factors (VIFs), and they were below the collinearity threshold ( $<2.5$ ) for all models (Dormann et al., 2013). Post-hoc tests were performed to distinguish among the effects of the three agricultural management regimes using the ‘emmeans’ package (Lenth, 2021). No deviations in model residuals for normality and homoscedasticity were observed. No spatial autocorrelation was found in models except for pest control (Fig. S3). We thus re-run model at 250 m for this proxy adding geographical coordinates (X, Y) as covariates. Finally, we estimated variance explained

using the pseudo-R<sup>2</sup> statistic (or R<sup>2</sup> when using the z-score transformation) of the full models (Nakagawa & Schielzeth, 2013).

### 3. Results

We collected 17,820 spiders, 10,963 carabid beetles (67 species), 8390 staphylinids, 3414 aphids, and 159 ladybird larvae (Table S3). We observed 4076 pollinating insects and 170 plant species.

#### 3.1. Comparison between hedgerows and crop fields

The value of the biodiversity-related multifunctionality index was higher for hedgerows than adjacent crop fields (Fig. 2; details of the GLMM results are presented in Table S4). Three of the four assessed proxies of ecological function were higher for hedgerows than crop fields (Fig. 2). No difference in pollination function proxy was observed between hedgerows and crop fields. These results hold true regardless of standardisation method for multifunctionality index, while values of the pollination and pest infestation functions were similar for hedgerows and fields when using the z-score transformation; Table S5).

#### 3.2. Comparison between agricultural management

Values for the agroecosystem multifunctionality index were lower for CF fields than OF Mixed crops, but no significant differences were found between CF fields and OF Cereal crops (Fig. 3; Table S6). Difference between CF and OF Mixed crops was no longer significant when using the z-score transformation (Table S7).

Focusing on ecological performance, values for the proxies of conservation and pollination functions were found to be significantly higher for OF (Cereal crops and Mixed crops) than CF fields. Higher values for the pest control proxy were obtained for OF Mixed crops, whereas no significant difference was observed between OF Cereal crops and CF fields.



Higher values of the pest infestation proxy were obtained for OF Mixed crops fields than for CF fields (Fig. 3). Pollination was identified as the proxy showing the greatest difference among agricultural management types, ranging from  $0.002 \pm 0.008$  for CF fields to  $0.53 \pm 0.37$  for the OF Cereal crops (Fig. 3). Focusing on agronomic performance, crop yields were higher for CF than OF (Cereal crops and Mixed crops) fields (Fig. 3; Table S6). Higher values for labour were obtained for OF Cereal crops than for CF fields, whereas no significant difference was observed between OF Mixed crops and CF fields. No significant difference among CF and OF was observed with respect to semi-net margin (Fig. 3; Table S6). Similar results were obtained with the z-score transformation except for labour (Table S7). Significant difference in labour among agricultural management types was no longer observed with the z-score transformation.

### **3.3. Relative effects of local farming system and landscape heterogeneity**

Local farming system had a significant and overriding impact on ecological and agronomic performances of agroecosystems, but did not influence their socio-economic performance nor their multifunctionality. Proxies for ecological functions had higher values for OF than CF, while crop yields were lower for OF than CF (Table 1). Overall, no landscape effects were observed (Table 1). No significant effect of landscape metrics on the agroecosystem multifunctionality index were observed, regardless of the spatial scale considered or the standardisation methods used (Tables S8-9). The amount of semi-natural habitat (% SNH) was significantly and positively correlated with biodiversity conservation at 500 m and 1000 m with the z-score transformation while no significant effect was detected with standardisation using the maximum value (Tables S8-9). The amount of semi-natural habitat (% SNH) also had a significant and positive effect on the pest control function at 500 m (Table S9), but this effect was no longer observed following standardisation using the maximum value (Table S8). No significant landscape effects were observed on socio-economic nor agronomic performance,

and this result hold true regardless of the standardisation method used for indices (Tables S8-9).

#### 4. Discussion

In this study, by combining a global assessment of the multifunctionality (aggregated index) and proxies of the ecological, socio-economic, and agronomic performance of ecosystems, we were able to identify broad trends in the effects of hedgerows and OF at local and landscape scales on the multiple performances of ecosystems in agricultural landscapes.

At the local scale, we detected higher biodiversity-related multifunctionality for hedgerows than for crop fields. This is consistent with the findings of previous studies that focused on individual taxa or functions, and that highlighted higher species diversity of spiders (Mestre et al., 2018) and higher levels of pest control in hedgerows compared to crop fields (Morandin et al., 2016; Van Vooren et al., 2017). The higher ecological value of hedgerows can be explained by the lower levels of disturbance they suffer compared with crops. Hedgerows are not ploughed and rarely chemically treated, which are practices that have detrimental effects on arthropods and plants (Holland & Reynolds, 2003; Zaller & Brühl, 2021). However, hedgerows may be influenced to some extent by chemical drift. Unlike fields, hedgerows are typically characterised by a complex structure, comprising diverse vegetal strata, high-quality floral resources over time, dead wood, and a stony ground cover, together providing suitable habitat conditions and/or diverse food resources for ground-dwelling arthropods, pollinators and plants (Lecq et al., 2017; Dover, 2019). By promoting the diversity of natural enemies, hedgerows are also assumed to favour the natural control of pests that may infest adjacent fields (Van Vooren et al., 2017; Mestre et al., 2018), although in this regard, our observations of high pest abundance (aphids and troublesome weeds) in hedgerows may counteract any beneficial effects. While previous work reported higher diversity of pollinators (Hannon & Sisk, 2009) and higher levels of pollination in hedgerows (Morandin & Kremen, 2013) compared to crop fields, no

significant difference in pollination function proxy was observed here. This result could be explained by the fact that crop fields encompassed mixed crops, sown with legume species (Fabaceae) known to be particularly attractive for long-tongued pollinator species, i.e. most bumblebees and some solitary bees such as Apidae and Megachilidae (Cole et al., 2022).

Contrary to our expectations and previous studies (e.g. Wittwer et al., 2021), we did not find higher agroecosystem multifunctionality in OF fields than in CF fields. This result can be attributed to the antagonistic effects of organic farming on ecological and agronomic performances (Herzog et al. 2019). Our results indicated enhanced ecological performance of organically cultivated fields. Similar findings have been reported previously showing higher levels of pest control and pollination in OF fields, as a consequence of increases in the abundance of predatory arthropods and pollinators (Lichtenberg et al., 2017; Tamburini et al., 2020). The greater diversity and abundance of these beneficial taxa can be ascribed to the absence of chemical pesticide and mineral fertiliser inputs in organic systems, the use of which is known to have direct or indirect deleterious effects on above-ground biodiversity (Desneux et al., 2007; Sánchez-Bayo, 2021). By contrast, crop yields were notably lower in OF fields, thereby suggesting an antagonism between ecological and agronomic performance (Wittwer et al., 2021; Duflot et al., 2022). Such reductions in crop yields under OF can be explained, at least in part, by the accumulation of pathogens and troublesome weeds in the absence of pesticide application (Shennan et al., 2017), as observed in the present study. Interestingly, the lower yields in OF we observed were not mirrored by reductions in the semi-net margins obtained by farmers, indicating that in the context of our study, any economic losses due to reduced yields in OF can be offset by the price premiums commanded by organic products and lower input costs (Crowder & Reganold, 2015).

Contrary to expectations, we found that social performance related to labour (cumulative duration of interventions) was comparable under organic and conventional cultivation (Orsini

et al., 2018). The comparable levels of labour observed between organic and conventional fields could be associated with the calculation of this proxy *per se*, with interventions by organic farmers being less frequent but more prolonged. The duration of interventions might also have been underestimated for OF since manual weeding operations were not considered. Nevertheless, OF would appear to be advantageous in terms of farmer workload, in addition to being more diversified and less repetitive than CF (Jansen, 2000). Moreover, in general, higher levels of farmer satisfaction (e.g. health, work satisfaction, and social recognition) are reported among those engaged in OF (Shennan et al., 2017).

Further in-depth analysis of agricultural management in OF revealed higher values for biodiversity conservation and pest regulation in systems cultivating mixed legume-cereal crops than on farms monocropping cereals. This could be attributed to the provision of abundant floral resources (during the blooming of faba beans and peas) for nectar-consuming natural enemies (Beyer et al., 2020), as well as a more favourable microclimate and complex vegetation structure that provides shelter for certain natural enemies (De Heij et al., 2022). Our results also highlighted differences in social and economic performances according to agricultural management, but only when using the standardisation by the maximum value. OF cereal crops were characterised by higher labour than the two other management types, indicating that they were less advantageous in terms of farmer workload in comparison with CF crops and OF mixed crops. This result can be explained by the fact that organic crops rely on frequent mechanical weeding for weed control (Bondy & Grundy, 2001). However, in mixed crops with legumes, mechanical interventions are difficult, even not possible, due to differences in growth stage of the two sown species (Bedoussac et al., 2015). Organic mixed crops had also lower economic performance than organic cereal crops, probably because they are specifically grown by farmers for animal feeding. These findings accordingly underline the importance of taking into account the diversity of agricultural practices in OF to better understand the drivers of the

multiple performances of agroecosystems (Puech et al., 2014). The similar value of agroecosystem multifunctionality index between the three management types can again probably be explained by the fact that we averaged functions during index calculation (i.e. mixing high ecological performance with reduced yields in OF Cereal crops).

Most studies that have sought to integrate the landscape level in analyses of ecosystem multifunctionality have involved a global assessment of land-use scenarios (e.g. Gong et al., 2019), but without due consideration of ecological, socioeconomic and agronomic performance simultaneously, although recent research points in this direction (Martin et al., 2019; Sirami et al., 2019). To the best of our knowledge, the present study is the first to investigate the effects of landscape heterogeneity related to semi-natural habitat (% SNH and hedgerow density) and farming practices (% OF) on multifunctionality. We predicted higher agroecosystem multifunctionality in landscapes with a high density of hedgerows and extent of OF, as a consequence of enhanced ecological (Holzschuh et al., 2008; Muneret et al., 2019; Zirbel et al., 2019) and agronomic (Redhead et al., 2020) performance. However, in contrast to expectations, our findings indicate that landscape heterogeneity had no appreciable influence on multifunctionality. The amount of semi-natural habitat had a positive effect on biodiversity conservation when using the z-score transformation. Although our biodiversity conservation index was composed of three taxa only and was restricted to above-ground biodiversity, this result provides additional evidence that increasing the amount of semi-natural cover in the landscape enhances local diversity in agroecosystems (Tschardt et al., 2005). We also showed that the extent of organic farming did not have any effect on multifunctionality nor performances. Care must be taken when considering this result because confounding factors might occur despite our effort. We cannot fully disentangle the amount of organic farming in the immediate vicinity of fields from farming systems (i.e. aggregation of fields under organic farming at small scales; Fig. S2). Finally, we did not observe any effect of landscape

configuration related to hedgerow density. This result might reflect the contrasting responses of the studied taxa, given that hedgerows can serve as either a barrier or corridor to species dispersal, as demonstrated for carabid beetles, plants and pollinator guilds (Mauremooto, 1995; Krewenka et al., 2011; Klaus et al., 2015; Vanneste et al., 2020). Another explanation may come from the truncated gradient of hedgerow density towards high values. Indeed, our study area was characterised by a dense hedgerow network (bocage). It is therefore possible that our hedgerow density gradient was not broad enough to observe significant responses.

Lastly, the ‘averaging’ approach employed here produces a single metric to estimate the multifunctionality index by averaging the values of all standardised ecosystem functions. Using two standardisation methods (maximum value *vs.* z-score), we showed that our main results hold true, underlining their robustness. Nevertheless, the antagonistic responses of individual functions underline the limitation in calculating a single aggregated index to assess the effects of environmental drivers on ecosystem multifunctionality, as highlighted by Byrnes et al. (2014). We advocate that such an approach, in which functions are assumed to be substitutable, is indissociable from a ‘function by function’ analysis to elucidate trade-offs and synergies among ecosystem functions, and provide more reliable information for management and decision-making processes.

## 5. Conclusion

To meet multiple societal expectations regarding environmental preservation, agricultural efficiency, and the maintenance of human well-being, it is necessary to develop management approaches that enhance the multifunctionality of ecosystems and, at broader spatial scales, of agricultural landscapes (Stürck & Verburg, 2017). This represents a considerable challenge, given that it requires not only identifying management options that simultaneously target the ecological, agronomic and socio-economic performance of ecosystems, but also the appropriate scales at which to implement them (Marja et al., 2022).

By investigating the effects of semi-natural habitat and farming systems at local and landscape scales, our study provides insights on their potential contributions to sustaining multifunctionality within agricultural landscapes. We found that hedgerows represent valuable semi-natural habitats at the local scale and contribute to enhancing ecosystem multifunctionality, owing to their higher importance for biodiversity conservation and associated ecological functions compared with cultivated fields. We also demonstrated that cultivation of organic crops has higher ecological performance but lower agronomic performance than cultivation of conventional crops resulting in similar levels of agroecosystem multifunctionality. Planting hedgerows and expanding organic farming are two key elements among a diverse collection of agri-environment schemes (AESs) developed in Europe to counteract the detrimental environmental effects of intensive agriculture. Our current findings highlight that these two AESs are potentially effective tools that can make a valuable contribution to promoting ecological performance underlying multifunctionality in agricultural landscapes, particularly in the bocage-type landscapes characteristic of north-western Europe. However, our observations also underline the fact that the adoption of organic practices on farms might necessitate trade-offs between crop productivity and ecological benefits. Moreover, the apparent lack of any significant multifunctionality-associated effects of hedgerows and organic farming at the landscape scale would tend to indicate that local agricultural fields and adjacent margins represent pertinent levels of management for the implementation of these AESs on farms.

#### **Authors' contributions**

Audrey Alignier, Stéphanie Aviron, Julien Pétilon, and Eloïse Couthouis conceived the study; Audrey Alignier and Stéphanie Aviron obtained funding; Eloïse Couthouis, Audrey Alignier, and Stéphanie Aviron performed data collection and curation, and identified species; Eloïse Couthouis, Audrey Alignier and Stéphanie Aviron analysed the data; Eloïse Couthouis, Audrey

Alignier, Stéphanie Aviron, and Julien Pétilon wrote the manuscript. All authors contributed critically to the manuscript and gave final approval for publication.

## **Acknowledgements**

We warmly thank Philippe Knapen, Jean-Luc Roger, Gérard Savary, Arnaud Maillard, Clovis Ragot, Sapho-Lou Marti, Laurie Civel, Nathan Lenestour and Nicolas Thomas for their essential contributions to the field work, farmer interviews and identification of taxa. We thank Sébastien Boinot for advice on statistical analysis as well as both reviewers and associate editor for their helpful comments on the earlier version of the manuscript. Finally, we also thank the farmers who kindly allowed us to collect samples in their fields. This work was funded by the Fondation de France under the ‘Research on agroforestry’ framework.

## **Conflicts of interest**

The authors declare that they have no conflicts of interest.

## **Data availability statement**

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.k98sf7m8z> (Couthouis et al., 2022).

## **References**

Bartoń, K. (2020). Multi-Model Inference [R package MiMIn version 1.43.17] [WWW Document]. URL <https://CRAN.R-project.org/package=MuMIn> (accessed 6.15.21)



- Baudry, J., Bunce, R.G.H., & Burel, F. (2000). Hedgerows: An international perspective on their origin, function and management. *Journal of Environmental Management* 60, 7–22. <https://doi.org/10.1006/jema.2000.0358>
- Bedoussac, L., Journet, E. P., Hauggaard-Nielsen, H., Naudin, C., Corre-Hellou, G., Jensen, E. S., Prieur, L. & Justes, E. (2015). Ecological principles underlying the increase of productivity achieved by cereal-grain legume intercrops in organic farming. A review. *Agronomy for Sustainable Development* 35(3), 911-935. <https://doi.org/10.1007/s13593-014-0277-7>
- Benton, T.G., Vickery, J.A., & Wilson, J.D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution* 18, 182–188. [https://doi.org/10.1016/S0169-5347\(03\)00011-9](https://doi.org/10.1016/S0169-5347(03)00011-9)
- Beyer, N., Gabriel, D., Kirsch, F., Schulz-Kesting, K., Dauber, J., & Westphal, C. (2020). Functional groups of wild bees respond differently to faba bean *Vicia faba* L. cultivation at landscape scale. *Journal of Applied Ecology* 57, 2499–2508. <https://doi.org/10.1111/1365-2664.13745>
- Bond, W., & Grundy, A. C. (2001). Non-chemical weed management in organic farming systems. *Weed Research* 41(5), 383-405. <https://doi.org/10.1046/j.1365-3180.2001.00246.x>
- Botzas-Coluni, J., Crockett, E.T.H., Rieb, J.T., & Bennett, E.M. (2021). Farmland heterogeneity is associated with gains in some ecosystem services but also potential trade-offs. *Agriculture, Ecosystems & Environment* 322, 107661. <https://doi.org/10.1016/j.agee.2021.107661>

- Boussard, H., Meurice, P., & Baudry, J. (2020). Chloe - Landscape Metrics: a software for landscape pattern analysis. QGIS plug in produced by the authors at the BAGAP unit, Rennes, France. Available at the following web site. <https://www6.rennes.inrae.fr/bagap/PRODUCTIONS/Logiciels> (accessed 8.6.2021)
- Brooks, M., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Benthem, K., Bolker, B., Sadat, N., Lüdecke, D., Lenth, R., O'Brien, J., & Magnusson, A. (2020). Generalized Linear Mixed Models using Template Model Builder [R package glmmTMB version 1.0.2.1]
- Burnham, K.P., Anderson, D.R., & Huyvaert, K.P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* 65, 23–35. <https://doi.org/10.1007/s00265-010-1029-6>
- Byrnes, J.E.K., Gamfeldt, L., Isbell, F., Lefcheck, J.S., Griffin, J.N., Hector, A., Cardinale, B.J., Hooper, D.U., Dee, L.E. and Emmett Duffy, J. (2014), Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. *Methods in Ecology and Evolution* 5, 111-124. <https://doi.org/10.1111/2041-210X.12143>
- Cade, B.S. (2015). Model averaging and muddled multimodel inferences. *Ecology* 96, 2370–2382. <https://doi.org/10.1890/14-1639.1>
- Chaplin-Kramer, R., O'Rourke, M. E., Blitzer, E. J., & Kremen, C. (2011). A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology letters* 14(9), 922-932. <https://doi.org/10.1111/j.1461-0248.2011.01642.x>

- Cole, L.J., Baddeley, J.A., Robertson, D., Topp, C.F.E, Walker, R.L., & Watson, C.A. (2022). Supporting wild pollinators in agricultural landscapes through targeted legume mixtures. *Agriculture, Ecosystems and Environment* 323(1), 107648. <https://doi.org/10.1016/j.agee.2021.107648>
- Couthouis, E., Aviron, S., Pétilion, J., Alignier, A. (2022). Data from: Ecosystem multifunctionality is promoted by organic farming and hedgerows at the local scale but not at the landscape scale. Dryad Digital Repository, <https://doi.org/10.5061/dryad.k98sf7m8z>
- Crowder, D.W., & Reganold, J.P. (2015). Financial competitiveness of organic agriculture on a global scale. *Proceedings of the National Academy of Sciences of the United States of America* 112, 7611–7616. <https://doi.org/10.1073/pnas.1423674112>
- Dainese, M., Martin, E.A., Aizen, M.A., et al. (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *Science Advances* 5(10), eaax0121. <https://doi.org/10.1126/sciadv.aax0121>
- Dainese, M., Montecchiari, S., Sitzia, T., Sigura, M., & Marini, L. (2017). High cover of hedgerows in the landscape supports multiple ecosystem services in Mediterranean cereal fields. *Journal of Applied Ecology* 54, 380–388. <https://doi.org/10.1111/1365-2664.12747>
- De Heij, S.E., Benaragama, D., & Willenborg, C.J. (2022). Carabid activity-density and community composition, and their impact on seed predation in pulse crops. *Agriculture, Ecosystems & Environment* 326, 107807. <https://doi.org/10.1016/j.agee.2021.107807>

584 Desneux, N., Decourtye, A., & Delpuech, J.M. (2007). The sublethal effects of pesticides on  
 585 beneficial arthropods. *Annual Review of Entomology* 52, 81–106.  
 586 <https://doi.org/10.1146/annurev.ento.52.110405.091440>

587 Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G.,  
 588 Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E.,  
 589 Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. and Lautenbach, S. (2013),  
 590 Collinearity: a review of methods to deal with it and a simulation study evaluating their  
 591 performance. *Ecography* 36, 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>

592 Dover, J.W. (2019) *The Ecology of Hedgerows and Field Margins*. Routledge, Abingdon,  
 593 OXon, New York, NY.

594 Dufлот, R. San-Cristóbal, M. Andrieu, E. Choisis, J.P., Esquerré, D. Ladet, S., Ouin, A., Rivers-  
 595 Moore, J., Sheeren, D., Sirami, C., Fauvel, M., & Vialatte, A. (2022). Farming intensity  
 596 indirectly reduces crop yield through negative effects on agrobiodiversity and key  
 597 ecological functions. *Agriculture, Ecosystems & Environment* 326, 107810.  
 598 <https://doi.org/10.1016/j.agee.2021.107810>

599 Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena,  
 600 G.M., & Martin, J.L (2011). Functional landscape heterogeneity and animal biodiversity  
 601 in agricultural landscapes. *Ecology Letters* 14, 101–112. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2010.01559.x)  
 602 [0248.2010.01559.x](https://doi.org/10.1111/j.1461-0248.2010.01559.x)

603 Fusser, M.S., Pfister, S.C., Entling, M.H., & Schirmel, J. (2016). Effects of landscape  
 604 composition on carabids and slugs in herbaceous and woody field margins. *Agriculture,*  
 605 *Ecosystems & Environment* 226, 79–87. <https://doi.org/10.1016/j.agee.2016.04.007>

- Garratt, M.P.D., Senapathi, D., Coston, D.J., Mortimer, S.R., & Potts, S.G. (2017). The benefits of hedgerows for pollinators and natural enemies depends on hedge quality and landscape context. *Agriculture, Ecosystems & Environment* 247, 363–370.  
<https://doi.org/10.1016/j.agee.2017.06.048>
- Gong, J., Liu, D., Zhang, J., Xie, Y., Cao, E., & Li, H. (2019). Tradeoffs/synergies of multiple ecosystem services based on land use simulation in a mountain-basin area, western China. *Ecological Indicators* 99, 283–293.  
<https://doi.org/10.1016/j.ecolind.2018.12.027>
- Hannon, L.E., & Sisk, T.D. (2009). Hedgerows in an agri-natural landscape: Potential habitat value for native bees. *Biological Conservation* 142, 2140–2154.  
<https://doi.org/10.1016/j.biocon.2009.04.014>
- Herzog, C., Honegger, A., Hegglin, D., Wittwer, R., de Ferron, A., Verbruggen, E., Jeanneret, P., Schlöter, M., Banerjee, S., & van der Heijden, M. G. A. (2019). Crop yield, weed cover and ecosystem multifunctionality are not affected by the duration of organic management. *Agriculture, Ecosystems & Environment* 284, 106596.  
<https://doi.org/10.1016/j.agee.2019.106596>
- Holland, J.M., & Reynolds, C.J.M. (2003). The impact of soil cultivation on arthropod (Coleoptera and Araneae) emergence on arable land. *Pedobiologia* 47, 181–191.  
<https://doi.org/10.1078/0031-4056-00181>
- Hölting, L., Beckmann, M., Volk, M., & Cord, A.F. (2019). Multifunctionality assessments - More than assessing multiple ecosystem functions and services? A quantitative literature review. *Ecological Indicators* 103, 226–235.  
<https://doi.org/10.1016/j.ecolind.2019.04.009>

- Holzschuh, A., Steffan-Dewenter, I., & Tschardtke, T. (2008). Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos* 117, 354–361. <https://doi.org/10.1111/j.2007.0030-1299.16303.x>
- Jansen, K. (2000). Labour, livelihoods and the quality of life in organic agriculture in Europe. *Biological Agriculture & Horticulture* 17, 247–278. <https://doi.org/10.1080/01448765.2000.9754845>
- Jolys, O., Dubuc, M., Ancelet, E., & Munier-Jolain, N. (2016). Agrosyst: Guide de l'utilisateur, version 2.1
- Klaus, F., Bass, J., Marholt, L., Müller, B., Klatt, B., & Kormann, U. (2015). Hedgerows have a barrier effect and channel pollinator movement in the agricultural landscape. *Journal of Landscape Ecology* 8, 22–31. <https://doi.org/10.1515/jlecol-2015-0001>
- Krewenka, K.M., Holzschuh, A., Tschardtke, T., & Dormann, C.F. (2011). Landscape elements as potential barriers and corridors for bees, wasps and parasitoids. *Biological Conservation* 144, 1816–1825. <https://doi.org/10.1016/j.biocon.2011.03.014>
- Lecq, S., Loisel, A., Brischoux, F., Mullin, S.J., & Bonnet, X. (2017). Importance of ground refuges for the biodiversity in agricultural hedgerows. *Ecological Indicators* 72, 615–626. <https://doi.org/10.1016/j.ecolind.2016.08.032>
- Lenth, R.V. (2021). Estimated Marginal Means, aka Least-Squares Means [R package emmeans version 1.6.1] [WWW Document]. URL <https://CRAN.R-project.org/package=emmeans> (accessed 6.15.21)
- Lichtenberg, E.M., Kennedy, C.M., Kremen, C., et al. (2017). A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across

agricultural landscapes. *Global Change Biology* 23, 4946–4957.  
<https://doi.org/10.1111/gcb.13714>

Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M. et al.  
(2012) Plant species richness and ecosystem multifunctionality in global drylands.  
*Science* 335, 214–218. <https://doi.org/10.1126/science.1215442>

Manning, P., van der Plas, F., Soliveres, S., Allan, E., Maestre, F.T., Mace, G., Whittingham,  
M.J., & Fischer, M. (2018). Redefining ecosystem multifunctionality. *Nature Ecology  
& Evolution* 2, 427–436. <https://doi.org/10.1038/s41559-017-0461-7>

Marja, R., Tschardtke, T., & Batáry, P. (2022). Increasing landscape complexity enhances  
species richness of farmland arthropods, agri-environment schemes also abundance - A  
meta-analysis. *Agriculture, Ecosystems & Environment* 326.  
<https://doi.org/10.1016/j.agee.2021.107822>, [107822](https://doi.org/10.1016/j.agee.2021.107822)

Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., ... & Steffan-  
Dewenter, I. (2019). The interplay of landscape composition and configuration: new  
pathways to manage functional biodiversity and agroecosystem services across Europe.  
*Ecology letters* 22(7), 1083-1094. <https://doi.org/10.1111/ele.13265>

Martin, E.A., Seo, B., Park, C.R., Reineking, B., & Steffan-Dewenter, I. (2016). Scale-  
dependent effects of landscape composition and configuration on natural enemy  
diversity, crop herbivory, and yields. *Ecological Applications* 26, 448–462.  
<https://doi.org/10.1890/15-0856>

Mauremooto, J. (1995). Permeability of hedgerows to predatory carabid beetles. *Agriculture,  
Ecosystems & Environment* 52, 141–148. [https://doi.org/10.1016/0167-8809\(94\)00548-S](https://doi.org/10.1016/0167-8809(94)00548-S)

- Mestre, L., Schirmel, J., Hetz, J., Kolb, S., Pfister, S.C., Amato, M., Sutter, L., Jeanneret, P., Albrecht, M., & Entling, M.H. (2018). Both woody and herbaceous semi-natural habitats are essential for spider overwintering in European farmland. *Agriculture, Ecosystems & Environment* 267, 141–146. <https://doi.org/10.1016/j.agee.2018.08.018>
- Montgomery, I., Caruso, T., & Reid, N. (2020). Hedgerows as ecosystems: Service delivery, management, and restoration. *Annual Review of Ecology, Evolution, & Systematics* 51, 81–102. <https://doi.org/10.1146/annurev-ecolsys-012120-100346>
- Morandin, L. A., & Kremen, C. (2013). Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecological Applications* 23, 829-839. <https://doi.org/10.1890/12-1051.1>
- Morandin, L. A., Long, R. F., & Kremen, C. (2016). Pest control and pollination cost–benefit analysis of hedgerow restoration in a simplified agricultural landscape. *Journal of Economic Entomology* 109, 1020-1027. <https://doi.org/10.1093/jee/tow086>
- Mouillot, D., Villegier, S., Scherer-Lorenzen, M. & Mason, N.W.H. (2011) Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE* 6, e17476. <https://doi.org/10.1371/journal.pone.0017476>
- Muneret, L., Auriol, A., Thiéry, D., & Rusch, A. (2019). Organic farming at local and landscape scales fosters biological pest control in vineyards. *Ecological Applications* 29, e01818. <https://doi.org/10.1002/eap.1818>
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4, 133-142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>



- Orsini, S., Padel, S., & Lampkin, N. (2018). Labour use on organic farms: A review of research since 2000. *Organic Farming* 4, 7–15. <https://doi.org/10.12924/of2018.04010007>
- Puech, C., Baudry, J., Joannon, A., Poggi, S., & Aviron, S. (2014). Organic vs. conventional farming dichotomy: Does it make sense for natural enemies? *Agriculture, Ecosystems & Environment* 194, 48–57. <https://doi.org/10.1016/j.agee.2014.05.002>
- Puech, C., Poggi, S., Baudry, J., & Aviron, S. (2015). Do farming practices affect natural enemies at the landscape scale? *Landscape Ecology* 30, 125–140. <https://doi.org/10.1007/s10980-014-0103-2>
- Redhead, J.W., Oliver, T.H., Woodcock, B.A., & Pywell, R.F. (2020). The influence of landscape composition and configuration on crop yield resilience. *Journal of Applied Ecology* 57, 2180–2190. <https://doi.org/10.1111/1365-2664.13722>
- Roger, J.-L., Jambon, O., & Bouger, G. (2010). Clé de détermination des carabidés: Paysages agricoles de la Zone Atelier d'Armorique. Laboratoires INRA SAD-Paysage et CNRS ECOBIO, Rennes (in French), p. 256
- Sánchez-Bayo, F. (2021). Indirect effect of pesticides on insects and other arthropods. *Toxics* 9, 177. <https://doi.org/10.3390/toxics9080177>
- Sarthou, J.-P., Badoz, A., Vaissière, B., Chevallier, A., & Rusch, A. (2014). Local more than landscape parameters structure natural enemy communities during their overwintering in semi-natural habitats. *Agriculture, Ecosystems & Environment* 194, 17–28. <https://doi.org/10.1016/j.agee.2014.04.018>

- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology & Evolution* 1, 103–113. <https://doi.org/10.1111/j.2041-210X.2010.00012.x>
- Shennan, C., Krupnik, T.J., Baird, G., Cohen, H., Forbush, K., Lovell, R.J., & Olimpi, E.M. (2017). Organic and conventional agriculture: A useful framing? *Annual Review of Environment & Resources* 42, 317–346. <https://doi.org/10.1146/annurev-environ-110615-085750>
- Sirami, C., Gross, N., Baillod, A. B., Bertrand, C., Carrié, R., Hass, A., ... & Fahrig, L. (2019). Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proceedings of the National Academy of Sciences* 116, 16442–16447. <https://doi.org/10.1073/pnas.1906419116>
- Smith, O.M., Cohen, A.L., Reganold, J.P., Jones, M.S., Orpet, R.J., Taylor, J.M., Thurman, J.H., Cornell, K.A., Olsson, R.L., Ge, Y., Kennedy, C.M., & Crowder, D.W. (2020). Landscape context affects the sustainability of organic farming systems. *Proceedings of the National Academy of Sciences of the United States of America* 117, 2870–2878. <https://doi.org/10.1073/pnas.1906909117>
- Stürck, J., & Verburg, P.H. (2017). Multifunctionality at what scale? A landscape multifunctionality assessment for the European Union under conditions of land use change. *Landscape Ecology* 32, 481–500. <https://doi.org/10.1007/s10980-016-0459-6>
- Tamburini, G., Bommarco, R., Wanger, T.C., Kremen, C., van der Heijden, M.G.A., Liebman, M., & Hallin, S. (2020). Agricultural diversification promotes multiple ecosystem services without compromising yield. *Science Advances* 6, eab1715. <https://doi.org/10.1126/sciadv.ab1715>

- Tilman, D., Isbell, F., & Cowles, J.M (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, & Systematics* 45, 471–493. <https://doi.org/10.1146/annurev-ecolsys-120213-091917>
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecology Letters* 8(8), 857–874. <https://doi.org/10.1111/j.1461-0248.2005.00782.x>
- Tscharntke, T., Tylianakis, J.M., Rand, T.A., et al. (2012). Landscape moderation of biodiversity patterns and processes - Eight hypotheses. *Biological Reviews of the Cambridge Philosophical Society* 87, 661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>
- Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L.A., & Bengtsson, J. (2014). Land-use intensity and the effects of organic farming on biodiversity: A hierarchical meta-analysis. *Journal of Applied Ecology* 51, 746–755. <https://doi.org/10.1111/1365-2664.12219>
- Tutin, T.G., Burges, N.A., Chater, A.O., Edmondson, J.R., Heywood, V.H., Moore, D.M., Valentine, D.H., Walters, S.M., & Webb, D.A. (1993). *Flora europaea*. Cambridge University Press
- Valdés, A., Lenoir, J., Frenne, P.D., et al. (2019). High ecosystem service delivery potential of small woodlands in agricultural landscapes. *Journal of Applied Ecology* 57, 4–16. <https://doi.org/10.1111/1365-2664.13537>
- Van Vooren, L., Reubens, B., Broekx, S., De Frenne, P., Nelissen, V., Pardon, P., & Verheyen, P. (2017). Ecosystem service delivery of agri-environment measures: A synthesis for

hedgerows and grass strips on arable land. *Agriculture, Ecosystems & Environment* 244, 32–51. <https://doi.org/10.1016/j.agee.2017.04.015>

Van Vooren, L., Reubens, B., Ampoorter, E., Broekx, S., Pardon, P., Van Waes, C., & Verheyen, K. (2018). Monitoring the impact of hedgerows and grass strips on the performance of multiple ecosystem service indicators. *Environmental Management* 62, 241–259. <https://doi.org/10.1007/s00267-018-1043-4>

Vanneste, T., Govaert, S., De Kesel, W., et al. (2020). Plant diversity in hedgerows and road verges across Europe. *Journal of Applied Ecology* 57, 1244–1257. <https://doi.org/10.1111/1365-2664.13620>

Wittwer, R.A., Bender, S.F., Hartman, K., Hydbom, S., Lima, R., Audrey Alignier, V., Nemecek, T., Oehl, F., Olsson, P.A., Petchey, O., Prechsl, U.E., Schlaeppli, K., Scholten, T., Seitz, S., Six, J., & van der Heijden, M.G.A. (2021). Organic and conservation agriculture promote ecosystem multifunctionality. *Science Advances* 7, eabg6995. <https://doi.org/10.1126/sciadv.abg6995>

Wu, J., & David, J.L. (2002). A spatially explicit hierarchical approach to modeling complex ecological systems: Theory and applications. *Ecological Modelling* 153, 7–26. [https://doi.org/10.1016/S0304-3800\(01\)00499-9](https://doi.org/10.1016/S0304-3800(01)00499-9)

Zaller, J.G., & Brühl, C.A. (2021). Direct herbicide effects on terrestrial nontarget organisms belowground and aboveground Mesnage, R., Zaller, J.G. (Eds.), *Herbicides, emerging issues in analytical chemistry*. Elsevier, pp. 181–229. <https://doi.org/10.1016/B978-0-12-823674-1.00004-3>

783 Zeileis, A., Cribari-Neto, F., Gruen, B., Kosmidis, I., Simas, A.B., & Rocha, A.V. (2021). Beta  
784 Regression [R package betareg version 3.1-4] [WWW Document]. URL  
785 <https://CRAN.R-project.org/package=betareg> (accessed 6.15.21)

786 Zhang, W., Ricketts, T.H., Kremen, C., Carney, K., & Swinton, S.M. (2007). Ecosystem  
787 services and dis-services to agriculture. *Ecological Economics* 64, 253–260.  
788 <https://doi.org/10.1016/j.ecolecon.2007.02.024>

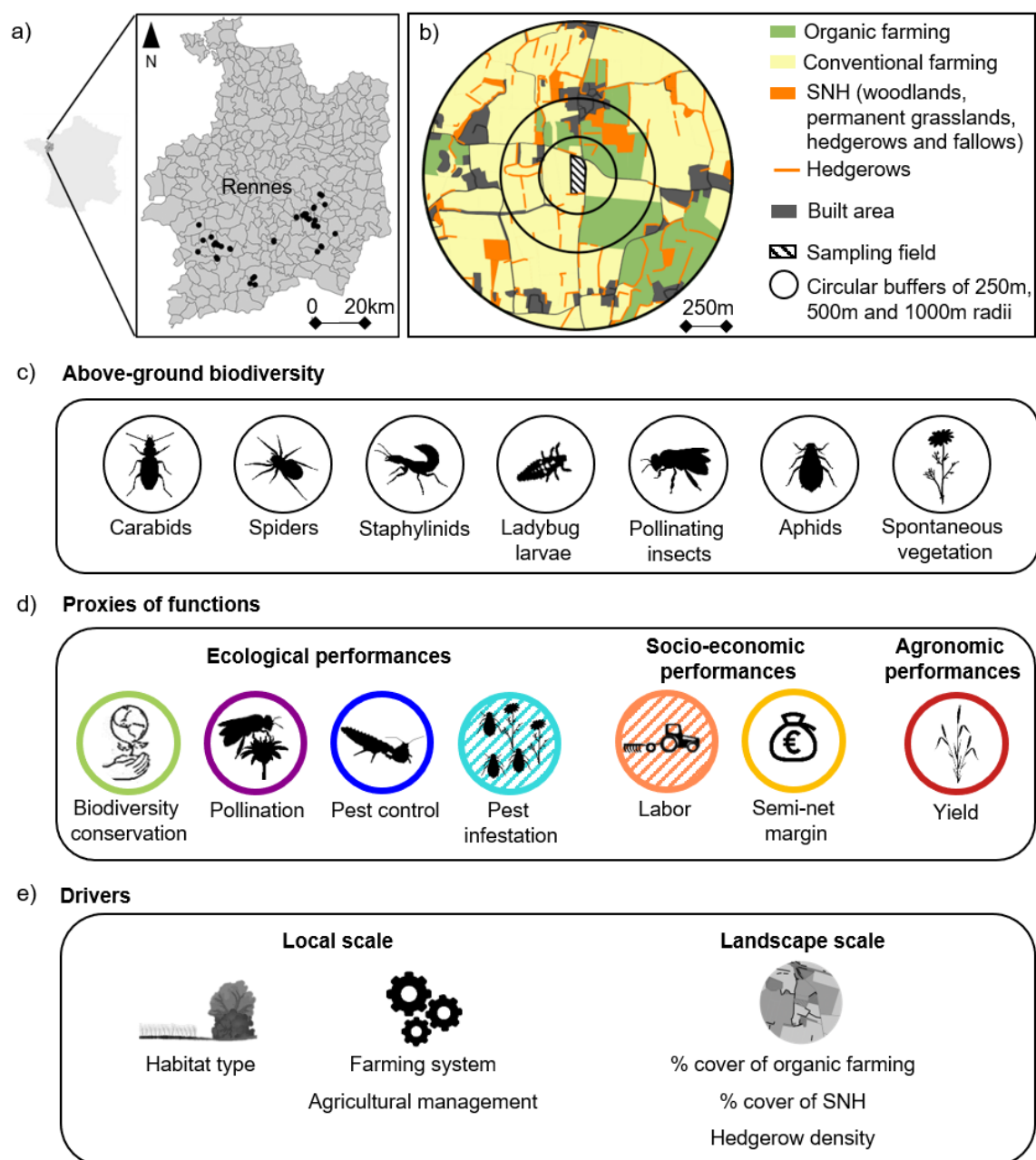
789 Zirbel, C.R., Grman, E., Bassett, T., & Brudvig, L.A. (2019). Landscape context explains  
790 ecosystem multifunctionality in restored grasslands better than plant diversity. *Ecology*  
791 100, e02634. <https://doi.org/10.1002/ecy.2634>

792 **Table 1.** Summary of the results from model averaging using generalised linear models (GLMs) for the effects of local farming system  
793 (conventional vs. organic) and landscape heterogeneity on the agroecosystem multifunctionality index (standardised by the maximum value) and  
794 individual functions. +, positive effect, -, negative effect, n.s., not significant. Brackets indicate the spatial scale for which the significant effect  
795 was observed. Where not mentioned, the significant effect was observed over all spatial scales. OF, organic farming; SNH, semi-natural habitats.  
796 For details, see Table S8.

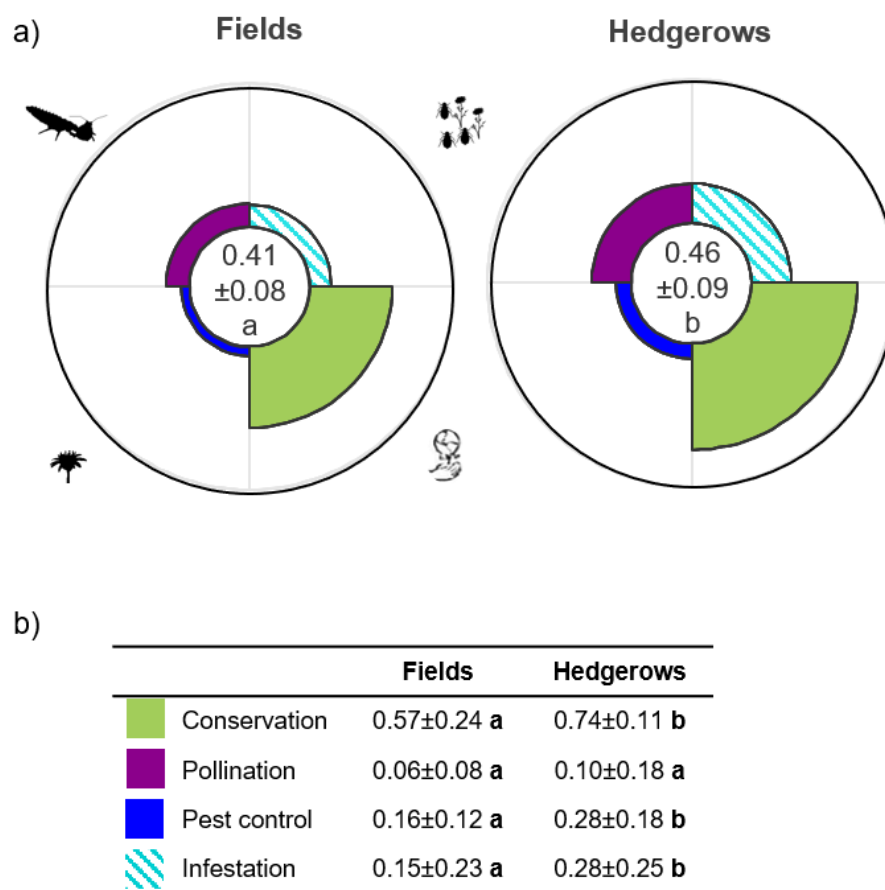
797

	Multifunctionality index	Ecological performance				Socio-economic performance		Agronomic performance
		Conservation	Pollination	Pest control	Pest infestation	Labour	Semi-net margin	Yield
Local OF	n.s.	+	+	+	+	n.s.	n.s.	-
% SNH	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
% OF	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Hedgerow density	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

798



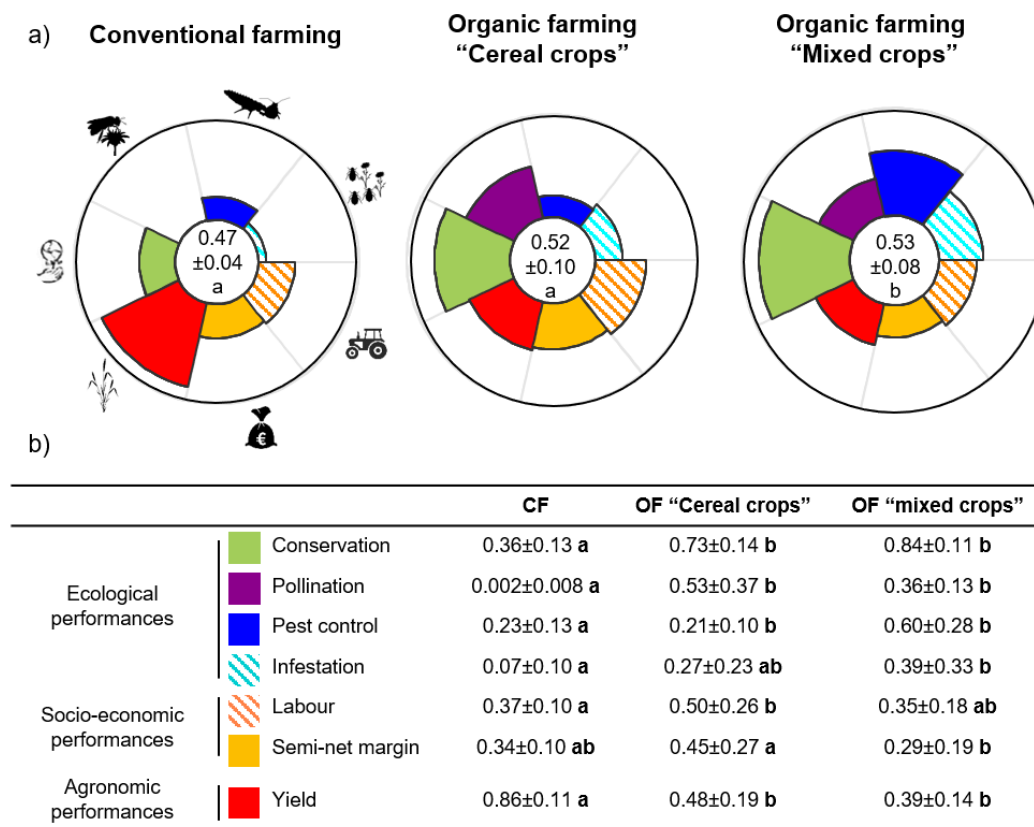
**Figure 1.** (a) Map showing the location of the 40 sampled fields and adjacent hedgerows in the study area. (b) Landscape mapping of farming systems and SNH. Three buffer radii (250 m, 500 m, 1000 m) were considered around sampled fields. (c) Details of the above-ground biodiversity studied. (d) Overview of proxies of the seven ecological, socio-economic and agronomic functions. The two hatched proxies of functions (infestation and labour) are those providing negative externalities. (e) Local and landscape drivers considered in the study. SNH, semi-natural habitats. Adapted from Valdés et al. (2019).



807

808 **Figure 2.** (a) Standardised proxies of ecological functions averaged for the two habitats studied  
809 (crop fields *vs.* hedgerows). Average values of the biodiversity-related multifunctionality index  
810 ( $\pm$  standard error, SE) are shown in the centre of the diagrams. Negative externalities are  
811 indicated by the hatched sectors and have been inverted for easier interpretation (i.e. the higher  
812 the proxy of the function, the lower the overall index of multifunctionality). (b) Means ( $\pm$  SE)  
813 of the standardised proxies of ecological functions. Different letters indicate significant  
814 differences between the two habitats (pairwise comparison with least squares means).





**Figure 3.** (a) Standardised proxies of ecological, socio-economic and agronomic functions according to agricultural management. Average values of the multifunctionality index ( $\pm$  SE) are shown in the centre of diagrams. Negative externalities are indicated by the hatched sectors and have been inverted for easier interpretation (i.e. the higher the function proxy, the lower the overall index of multifunctionality). (b) Mean values ( $\pm$  SE) of the standardised proxies of functions. Different letters indicate significant differences between agricultural management (pairwise comparison with least squares means calculated using the R package emmeans). NS, not significant; CF, conventional farming; OF, organic farming.