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Farming intensity indirectly reduces crop yield through negative effects on agrobiodiversity and key ecological functions☆

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ABSTRACT

Farming intensity and landscape heterogeneity influence agrobiodiversity and associated ecological functions. The relative contributions of these agroecosystem components to agricultural production remain unclear because of inter-relations and weather-dependant variations. Using a structural equation modelling approach, we estimated direct and indirect contributions of farming intensity (soil management, pesticide use and fertilisation) and landscape heterogeneity (of semi-natural covers and crop mosaic) to cereal crop production, in 54 fields (mostly wheat), in two years (24 and 30 fields). Indirect effects were evaluated through agrobiodiversity (carabid and plant communities) and ecological functions (pollination and pest control). In 2016, farming intensity had the largest direct positive effect on cereal crop yield, followed by agrobiodiversity (74% of the farming intensity impact) and ecological functions. However, the direct benefits of farming intensity were halved due to negative indirect effects, as farming intensity negatively affected within-field biodiversity and ecological functions. Overall, agrobiodiversity and farming intensity had equal net contributions to cereal crop yields, while heterogeneity of the crop mosaic enhanced biodiversity. In 2017, neither higher farming intensity nor agrobiodiversity and ecological functions could lift cereal production, which suffered from unfavourable meteorological conditions. Semi-natural habitats supported agrobiodiversity. Our study suggests that a reduction of farming intensity combined with higher heterogeneity of crop mosaic can enhance the benefits of ecological functions towards crop production. Semi-natural covers seem to play an essential role in the face of climatic events, by supporting agrobiodiversity and the potential resilience of the agroecosystem functioning.

1. Introduction

The worldwide model of intensive agriculture, as based on the "green revolution principles", relies on the use of agrochemical and mechanical inputs: pesticides, mineral fertilisers, and regular and deep ploughing. Meanwhile, farmed landscapes have been simplified, experiencing loss of semi-natural covers, increase in field size and reduction in crop diversity (Benton et al., 2003; Robinson and Sutherland, 2002). Such land-use intensification and homogenisation has caused many environmental issues (Tilman et al., 2002), including biodiversity loss in agroecosystems (*e.g.* Potts et al., 2016). Alternatively, the agroecological framework relies on biodiversity-driven ecological functions, defined as biological processes that ensure the agroecosystem functioning, particularly biological pest control and pollination (Duru et al., 2015; Garibaldi et al., 2018). There is therefore an apparent conflict between, on the one hand, the direct contribution of farming intensity and landscape simplification to crop yield, and on the other hand, their indirect harmful effects on the contribution of agrobiodiversity and related ecological functions. The relative contribution to crop yield of the direct and indirect effects of these productive factors remains unclear,

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undermining the transition towards agroecological production systems and implementation of adequate policy to encourage it (Rusch et al., 2010).

An additional challenge faced by agriculture is the vulnerability of agroecosystem functioning to environmental changes that occur at various spatiotemporal scales, such as outbreak of pests or other species invasions, extreme weather events, and climate change (*e.g.* gradual temperature increase). Persistence of ecological functions against these acute or chronic disturbances would provide stability in agricultural production across years (Martin et al., 2019b). For instance, plant diversity of grasslands was shown to increase resistance of productivity to climate extremes (Isbell et al., 2015).

Most beneficial species that contribute to ecological functions useful to farming require a combination of resources, *i.e.* feeding, reproduction and overwintering sites. The persistence of ecological functions depends on the availability of these resources within species home range (Schellhorn et al., 2015). Both local farming practices and landscape composition and configuration affect the availability, quality and accessibility of these resources, and strongly influence biodiversity in crop fields (Firbank et al., 2008; Kleijn et al., 2009). The central process is the spill-over of species from semi-natural covers to crop fields (and *vice versa*) or between crop fields of different types, allowing for landscape complementation, *i.e.* enabling beneficial species to access their required resources located at different place and time and adapt to recurrent disturbances (Aviron et al., 2018; Blitzer et al., 2012).

One of the main challenges for agroecological production systems is to identify the relative influence of various farming practices and aspects of landscape heterogeneity that would favour beneficial species (Holland et al., 2017; Rusch et al., 2010; Tscharntke et al., 2005) and the persistence of associated functions. At field level, farming practices, such as pesticide use or period of sowing or ploughing (which depend on crop type) determine the suitability of a crop, not only for phytophagous species (pests), but also for beneficial species. For instance, pesticide mixtures synergistically affect bee health (Siviter et al., 2021), while spring ploughing applied in spring crop fields such as maize has strong detrimental effects on carabid beetle communities (Purvis and Fadl, 2002), a taxa including beneficial predators. At landscape level, there is ample evidence that land-cover heterogeneity, and particularly of semi-natural covers, affects the supply of ecological functions sustained by agrobiodiversity (see meta-analyses of De Palma et al., 2016 and Duarte et al., 2018). The heterogeneity of crop mosaics may also provide different resources that promote agrobiodiversity and ecological functions (Baillod et al., 2017; Hass et al., 2018; Sirami et al., 2019). Landscape configuration plays a crucial role, as edges (or adjacencies) between different cover types facilitate spill-over and landscape complementation, and are often associated with higher arthropod diversity, biological control, pollination and crop yields (Martin et al., 2019a; Woodcock et al., 2016).

In the present study, we aimed at estimating the relative strength of direct and indirect effects of farming intensity (soil management, pesticide use, and nitrogen fertilisation), agrobiodiversity (carabid beetle and vascular plant communities), ecological functions (biological pest control and pollination), and landscape heterogeneity of semi-natural covers and of the crop mosaic on cereal crop production. To do so, we used a Partial Least Square – Path Modelling approach (PLS-PM), which was first developed in social sciences and recently applied in agroecological studies (Puech et al., 2015; Quinio et al., 2017). A conceptual model based on current knowledge of agroecosystem functioning (Table 1) was tested based on data collected in 54 winter cereal fields, in two years (24 and 30 fields respectively) that experienced contrasted meteorological conditions.

Table 1
Hypothesised effect (+/-) and justification for the conceptual path (inner) model tested in the Partial Least Square Path Models (PLS-PM).

Explanatory component	Dependent component	Hypothesised effect and justification
Farming intensity	Cereal production	(+) The primary objective of farming practices is to provide nutrition (*e.g.* nitrogen) and reduce competition and herbivory for the crops
Farming intensity	Local-field agrobiodiversity	(-) Farming intensity (especially of soil management and pesticide use) is known to affect biodiversity in crop fields, especially of arthropods and weeds (*e.g.* Geiger et al., 2010; Martin et al., 2020)
Land. Hetero. SNC Land. Hetero. crop mosaic	Local-field agrobiodiversity	(+) the presence of semi-natural covers and diverse crops is expected to be a strong driver of biodiversity in crop fields, as well as edges between land covers that enhance spill-over (*e.g.* Martin et al., 2020; Sirami et al., 2019)
Local-field agrobiodiversity	Pollination potential Pest control potential	(+) Carabid beetles are known predator of various pests and weeds, while plant diversity and abundance support pollinator communities (*e.g.* Bretagnolle and Gaba, 2015; Petit et al., 2018)
Pest control potential	Cereal production	(+) By suppressing pest pressure on crops, pest biological control can contribute to cereal production (Geiger et al., 2010)
Pollination potential	Cereal production	(+) Studied crops are not dependent on pollination. However, high pollination potential informs about the global agroecosystem health and landscape-wide intensity of farming practices, which can influence cereal production (Carrié et al., 2017; IPBES, 2016)
Farming intensity Land. Hetero. SNC Land. Hetero. crop mosaic	Pollination potential Pest control potential	(-/+) Local and landscape context affect ecological functions through agrobiodiversity, however, we expect multiple and complex mechanisms, not fully captured by our biodiversity measures (*e.g.* Holland et al., 2017; Rusch et al., 2010)
Local-field agrobiodiversity Land. Hetero. SNC Land. Hetero. crop mosaic	Cereal production	(+) Local-field agrobiodiversity and landscape context may enhance ecological functions not measured, *e.g.* soil properties, or not captured by the indirect measures of pollination and pest control, *e.g.* parasitism (Koivula, 2011; Martin et al., 2019a; McHugh et al., 2020)

2. Materials and methods

2.1. Study area and sites selection

The study took place in the Vallées et Coteaux de Gascogne (about 370 km^2), which is part of the Long-Term Socio-Ecological Research site LTSER ZA PYGAR, in south-western France (see Appendix S1: Fig. S1). This hilly region (250–400 m above sea level) is dominated by mixed crop-livestock farming where permanent grasslands are usually located

on slopes and annual crops (mostly wheat, barley and maize, but also rapeseed and sunflower) occupies the valleys (Ouin et al., 2021). Grasslands and crop fields are interspersed by small woodlands (mainly located on slopes) and few hedgerows. We selected 54 wheat, barley, or triticale crop fields in conventional farming systems to maximise variations in the proportion of wooded habitats within a 1 km^2 circular landscape surrounding them, ranging from 5% to 40% (see Appendix S1: Fig. S2). Average field size was 7.26+/- 4.28 ha. We sampled 24 and 30 fields, in 2016 and 2017 respectively. The two sampling years differed markedly in terms of meteorological conditions and were therefore analysed separately (see Appendix S1: Section S1). 2017 suffered from drought and local extreme storm events (heavy rain and wind), which affected crop yields. Indeed, 2017 experienced a cumulated 120 mm deficit in rainfall compared to 2016 over the first seven months of the year (380 and 501 mm respectively). In particular, there was a strong deficit in January, February, and in April, which is a key month for cereal productivity. Reduced rainfall was also combined with higher temperature in 2017, +2.1 and + 2.8 °C mean hourly air temperature in May and June (14.1 and 18 °C respectively in 2016).

2.2. Crop yield, ecological functions, and local-field agrobiodiversity

Within each crop field, all measures were performed along two 50 m-long transects, except for plant diversity monitoring (see below). The transects were parallel, 10 m apart from each other, and perpendicular to the field edge, starting 50 m apart from it (Fig. 1). The choice of field edge was mostly driven by convenience in relation to road access; however, we also avoided peculiar locations, such as adjacency with woodland.

Crop yield was estimated using six 50 cm × 50 cm plots per field, equally distributed along the two 50 m transects. Within each plot, all tillers were harvested. All seeds were extracted with a small threshing machine and weighed. Data were averaged across the six plots to calculate seed weight per hectare (hereafter crop yield).

Four types of predation potential (pest control) were measured with three different prey organisms (aphids, moth eggs and seeds), and using neutral-coloured (black) 5 cm × 5 cm predation paper "cards" (Geiger et al., 2010). Seed predation was assessed using *Viola arvensis* seeds (ten per card). Insect predation was assessed using aphids (*Acyrthosiphon pisum*, three per card) and moth eggs (*Ephestia kuehniella*, pack of bundle eggs because they are too small for exact enumeration). Preys were purchased from biocontrol companies that farm these organisms. Seeds, eggs and aphids (after being frozen to kill them) were glued to the cards using transparent, odourless glue (reference: UHU twist&glue ReNATURE solvent-free). Eggs and aphids cards were frozen until being placed in fields. For each predation measure, ten cards were equally distributed along the two 50 m transects. At each location, one card of seeds and one of aphids were nailed to the ground (hereafter ground position), and one card of moth eggs and one of aphids were stapled on the top of a crop plant, just under inflorescence (hereafter canopy position). While being placed in fields, predation cards were visually inspected to make sure no prey fell off; those with missing prey(s) were unused. Predation measures took place at the end of April and the end of May. For each period, aphid cards were left for 24 h in the field, while seed and egg cards were left for four days. Remaining seeds and aphids were counted directly in the field to calculate a predation rate (avoiding errors due to falling prey during manipulations). Eggs were too small and numerous to be counted, so we used a binocular magnifier in the lab to identify predation patterns: cards were considered predated if eggs completely or partially disappeared. Usually, signs of predation are visible: broken eggs or holes. Data were averaged per field across the ten locations and the two periods.

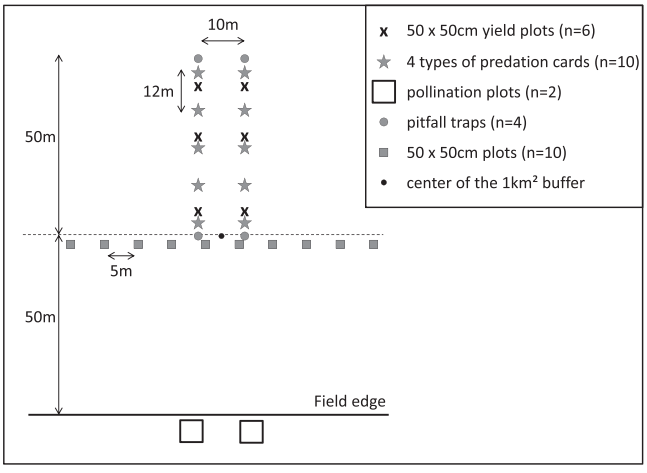


Fig. 1. Sampling design of ecological measurements as carried out in every selected crop fields.

Pollination potential was estimated using two plots of flowering strawberry plants located in field margins. Since the studied cereal crops are non-entomophilous and the measures made outside the fields, we did not estimate the potential crop pollination in the target field but a landscape-level pollination potential. In a context of crop successions that also include entomophilous crops (mainly oilseed rape and sunflower), we hypothesise that high landscape-level pollination potential for a given year reflects a favourable pollination context for subsequent entomophilous crops. We placed two control strawberry plants (protected by insect-proof bags) and two plants exposed to pollinators within each plot. Strawberry sprouts were grown in insect-proof glasshouses before the field experiment. Each flower that opened before or during field exposure was marked. Strawberry plants were left three days in the field and brought back to insect-proof glasshouses. Forty seeds were randomly collected from each fruit produced from marked flowers and tested for fertility. Seeds were put in water, floating seeds were considered unfertile, while those that sunk were considered fertile (Roselino et al., 2009). Data from the two plots were pooled to calculate the fertility ratio of exposed plants and the fertility gain, *i.e.* the difference in fertility ratio between exposed and control plants.

Agrobiodiversity was investigated through carabid beetle and vascular plant communities. Carabids play an important role as beneficial insects and are considered good ecological model for studying agrobiodiversity (Bohan et al., 2011, 2000). Vascular plants are well-known bioindicators of soil health, agricultural practices; and represent an important local food resource for may organisms (IPBES, 2016). Carabid beetle communities were assessed using four pitfall traps per field, *i.e.* one at each end of the two 50 m transects. Carabids were sampled during 4 days at the same time as the predation experiment. Carabids were identified to the species level (adapted from Roger et al., 2010). Data were pooled per field across the four traps and the two periods. Vascular plant communities were assessed using ten 50 cm × 50 cm plots located every five metres on a transect parallel to field edge (Fig. 1). In each plot, plant species relative covers were recorded as percentages of total plot area. All ten plots were pooled. Total species richness and Shannon diversity index were calculated for carabids and plants. In addition, total abundance (number of individuals) and total cover (%) were computed for carabids and plants respectively. Variation in species composition was also estimated for both taxonomic groups using the score of fields on the three first axes of a correspondence analysis performed on presence-absence data. Species appearing in less than 5% of fields were excluded from the correspondence analysis.

2.3. Farming practices

Farmers were interviewed in winter 2016 and 2017 to collect data on farming practices conducted in each sampled field. We collected data on three types of farming practices: soil management, pesticide use and

nitrogen fertilisation. The total number of operations was used as an overall proxy for farming intensity. The cumulated ploughing depth was used to describe soil management intensity. Fertilisation was calculated as an equivalent quantity of nitrogen in kilograms per hectare.

The Treatment Frequency Index (TFI) was calculated for all pesticide types together and for each separately: herbicides, insecticides, fungicides, in spraying as well as in coating. We considered the total TFI as intensity of pesticide use. Insecticides were not included as a separate variable in the final analyses, as their use was low in general, and did not vary much among farmers. TFI calculation takes into account the type of commercial product and the dose at which it was sprayed and quantifies the number of reference doses applied per hectare and per crop season (OECD, 2001):

$$TFI = \sum_{i=1}^{n} \frac{D_i \times S_i}{Dr_i \times S} \quad (1)$$

where D_i is the applied dose, S_i the treated surface area, Dr_i the reference dose obtained from the French Ministry of Agriculture online database (*ephy.anses.fr*), and S the total area of the field for each spraying operation i (Ricci et al., 2019).

We checked for potential correlations between measures of farming intensity, using Pearson correlation (Appendix S1: Fig. S4). As the amount of herbicide was the highest, it correlates with the total TFI (especially in 2017). All other correlations were < 0.7, often largely bellow.

2.4. Landscape heterogeneity metrics

Land-cover was digitised from field surveys and aerial orthophotos at 50 cm spatial resolution (named BDOrtho®) dating from 2012 and 2016 and produced by the French national mapping agency (IGN). Landscape-level metrics were calculated within 1-km^2 circles (*i.e.* within a 563 m-radius circular buffer, centred on the middle of ecological measurements, Fig. 1), using CHLOE2012 (Boussard and Baudry, 2014). We used nested three thematic resolutions to calculate 12 landscape metrics representing heterogeneity related to semi-natural covers (SNC heterogeneity) and to the crop mosaic (crop mosaic heterogeneity; graphical representations of these land-cover categories can be found in Appendix S1: Fig. S3). First, woodlands, hedgerows and permanent grasslands were grouped to calculate the proportion of SNC, the average patch size of SNC, the length of SNC edges, and the length of edges between SNC and crop fields. Second, additional land-cover categories were used: wooded habitats and permanent grasslands for SNC heterogeneity, spring crops (maize and sunflower), cereal winter crops (the studied crop type, wheat, triticale and barley), and other crops (oilseed rape and temporary grasslands) for crop heterogeneity. Winter crops are sown in autumn and harvested in early summer, while spring crops are sown in spring and harvested in late summer and early autumn. The proportion area of each category as well as the length of edges among all crop categories were calculated. Finally, we distinguished 16 different crop covers to calculate a Shannon crop diversity index based on the proportion of each crop cover. We used these land cover thematic resolutions to describe landscape functional heterogeneity that corresponds to the studied processes and to increase our ability to identify key elements (Fahrig et al., 2011). We checked for potential redundancy between landscape metrics using Pearson correlation (Appendix S1: Fig. S5). The most correlated variables were the amount of semi-natural cover, amount of permanent grassland and mean patch size of SNC (especially in 2016). All other correlations were < 0.7, often largely bellow.

2.5. Statistical analysis

We used a Partial Least Square Path Modelling (PLS-PM) approach that provides a comprehensive view of a system by modelling multiple relationships between its various components (Sanchez, 2013). Such hierarchical models explicitly account for interdependence among components (collinearity or co-existing patterns) and potential direct and indirect causal paths (Didham et al., 2012). More generally, PLS analysis is a multivariate method that is widely used to reduce the dimension of explanatory variables, and in case of multi-collinearity.

In the PLS-PM framework, a *latent variable* (LV) is viewed as a concept and is linked, in the so-called *outer* model, to a set of measurements (*manifest variables*, MV). In the reflexive mode (which we used here) MVs are the observed proxies of the concept represented by the LV and the LV is regressed on each MVs separately (Sanchez, 2013):

$$MV_{j,k} = \lambda_{0,k} + \lambda_{j,k} LV_j + error_{j,k} \quad (2)$$

where $MV_{j,k}$ is the k_{th} manifest variable of the j_{th} latent variable, and $\lambda_{j,k}$ are the regression coefficients (hereafter called *loadings*). As MVs are measures of the same latent unmeasurable phenomena, some collinearity between MVs that belong to the same LV is expected, and this contribute to create meaningful and coherent latent variables (Sanchez, 2013).

In this work, LVs included farming intensity (farmer's practices), landscape heterogeneity of semi-natural covers, landscape heterogeneity of the crop mosaic, local-field agrobiodiversity, pollination potential, pest control potential, and cereal production (see the complete list of variables in Appendix S1: Table S1). These seven LVs were linked by a conceptual model (named the inner model, or structural model, see Table 1 for justification) and translated as multiple linear regressions between LVs (Sanchez, 2013):

$$LV_j = \beta_{0,j} + \sum_i \beta_{i,j} LV_i + error_j \quad (3)$$

where LV_j is the j^{th} dependent latent variable, $\beta_{i,j}$ are the path coefficients, and LV_i are the explanatory variables of LV_j.

Following advices by Sanchez (2013), the PLS-PM was built through several steps. (i) A first model was fitted with a fixed inner model reflecting the agroecosystem functioning (Fig. 2) and all possible MVs. (ii) A second model was fitted to ensure unidimensionality of the LV. Indeed, all MVs pertaining to a LV need to be positively correlated to the LV. In practice, all MVs negatively correlated to their LV were transformed into their opposite. (iii) In a third model, MVs weakly correlated with their LV were removed, so that the MVs best reflect their LV. After several tries (not shown) we chose to remove MVs with a communality (cor^2 (LV, MV)) lower than 0.3 following Puech et al. (2015).

Two alternative conceptual models were investigated and are presented in Appendix S2. In the first alternative model, we removed the pollination potential latent variable, considering that studied cereal crop is not dependent on insect pollination (non-entomophilous crop). In the second alternative model, we considered local plant (weed) diversity alone, while carabids diversity measures were considered as measures of pest control along predation rate measures. The direct links from landscape heterogeneity of semi-natural cover and crop mosaic to cereal production were removed.

Model quality was evaluated by two indicators: the goodness-of-fit (GoF) as a trade-off between inner and outer models (average communality × average R-square of each block), and the R-square for dependent LVs. The *plspm* function in R (package PLSPM; Sanchez et al., 2017) computes *p*-values of a *t*-test for the null hypothesis of zero regression coefficient, for each multiple regression of the inner model. In addition, confidence level in regression coefficients within the outer and inner models were tested using a bootstrap procedure (200 iterations).

3. Results

For both years, the highest model fit was obtained for cereal production (R-square = 0.60 and 0.55 in 2016 and 2017 resp.), followed by local-field agrobiodiversity (R-square = 0.35 and 0.39 in 2016 and 2017 resp.). In 2016, pollination potential was well explained (R-square =

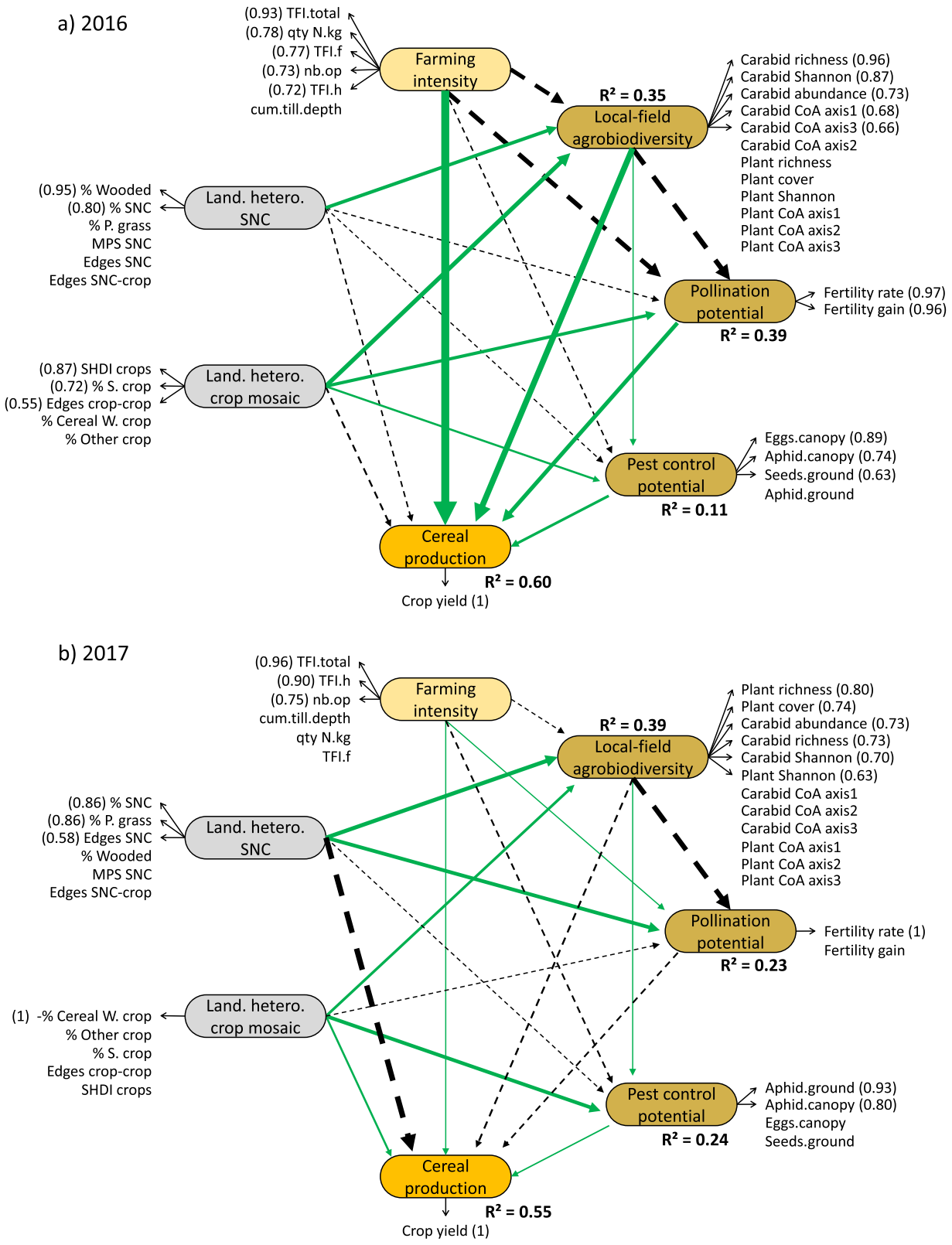


Fig. 2. Graphical illustration of the tested Partial Least Square Path Model (PLS-PM) in 2016 (a) and 2017 (b). For each latent variable (LV), represented by ovals, the manifest variables (MV) are sorted from higher to lower loading from top to down (value in brackets). All initially included MVs are shown, absence of arrows and loading value indicate MVs that were removed in the selection process. Coloured arrows display multiple regressions between LVs: green-solid and black-dashed arrows indicate positive and negative effects respectively, and arrows' thickness is proportional to the effect strength (regression coefficients, Table 2). Any LVs pointed out by one or several arrows is the dependent variable of a regression. LVs at the root of arrows are independent variables of one or more regressions. For a description of manifest variables, see Appendix S1: Table S1. Depending on the selected manifest variables, latent variables may have different interpretation between the two study years. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

0.39), while pest control potential showed lowest R-square (0.11). In 2017, pollination and pest control potentials showed poorer and better fits respectively (R-square = 0.23 and 0.24 resp.). Adequacy of the two models were satisfactory in terms of unidimensionality, communality, cross-loadings, and correlation between MVs and LVs (Appendix S1: Tables S2–4). Overall, goodness-of-fit was 0.49 in 2016 and 0.47 in 2017.

The number of manifest variables was reduced from 36 to 21 in 2016 and to 17 in 2017. The main differences between years were found in the local-field agrobiodiversity, and the SNC and the crop mosaic heterogeneity (Fig. 2a and b). It should be noted that total TFI (*i.e.* intensity of pesticide use) was significantly higher in 2017 than in 2016, especially the herbicide part, probably in reaction to higher levels of plant weed cover that year (Appendix S1: Table S1). In addition, crop yields were significantly lower in 2017 than in 2016, presumably due to drought and local storm events in spring. However, variability in TFI and crop yield within years were similar. Similar results as presented below were observed with the two alternative conceptual models (Appendix S2).

In 2016, farming intensity had a highly significant direct positive effect on cereal production and a significant negative effect on local-field agrobiodiversity and pollination potential (Table 2, Fig. 2a). Local-field agrobiodiversity had a negative effect on pollination potential, while local-field agrobiodiversity, pollination and pest control potentials had a positive influence on cereal production (Fig. 2a). These effects were significant except for the effect of pest control potential, which was marginally significant (p-value < 0.10, Table 2). As a result, farming intensity had both a positive direct effect on cereal production and a negative indirect effect through detrimental effect on agrobiodiversity and ecological functions (Fig. 3). Indirect negative effects were half as strong (53%) as direct positive effects. The total net effect of farming intensity and local-field agrobiodiversity on cereal production were of similar strength (0.41 *vs.* 0.43). In 2017, farming intensity did not have any effect on cereal production, local-field agrobiodiversity, and pollination and pest control potential, while the latter ones did not have any positive effect on cereal production (Fig. 2b, Table 2). Only the negative relationship between local-field agrobiodiversity and pollination potential remained significant.

In 2016, crop mosaic heterogeneity had, in general, a greater influence than SNC heterogeneity. Both had positive effects on local-field agrobiodiversity, although the latter only had a marginally significant effect (p-value < 0.10, Fig. 2a, Table 2). Crop mosaic heterogeneity also tend to influence positively pollination and pest control potential, although not significantly (Table 2). Consequently, crop mosaic heterogeneity had an indirect and net positive effect on cereal production, while SNC heterogeneity had a slightly negative effect (Fig. 3). In 2017, SNC heterogeneity and, to a lesser extent, crop mosaic heterogeneity (bootstrap only) had positive, significant effects on local-field agrobiodiversity. SNC heterogeneity also had a strong negative influence on cereal production and a marginally significant (p-value < 0.10) positive effect on pollination. In addition, crop mosaic heterogeneity had a marginally significant positive effect on pest control potential (p-value < 0.10).

4. Discussion

4.1. Farming intensity had positive direct and negative indirect effects on cereal production

Our results highlight the counter-productive effects of increased farming intensity within conventionally farmed crop fields. As expected, farming intensity (representing total pesticide use and nitrogen fertilisation) had a positive direct influence on cereal production in 2016 (Fig. 2a), although this was not true in 2017, which presented particular meteorological conditions (see year comparison below). However, the negative effects of farming intensity on local-field agrobiodiversity (representing the carabid community) and ecological functions indirectly reduced cereal production (Figs. 2a and 3). In turn, local-field agrobiodiversity and ecological functions positively influenced crop yield, and their combined contribution to cereal production was superior to the direct effect of farming intensity itself (Figs. 2a and 3). The balance between direct and indirect effects of farming intensity on cereal production shows that the benefits may be halved. Similarly, a recent meta-analysis demonstrated that low-input farming systems promote pest control to a level able to compensate the absence of pesticides use, despite higher levels of pest infestations (Muneret et al., 2018). Although the mechanisms underlying the direct and indirect effects of farming intensity on crop yield are very different, our results suggest that relaxing farming intensity in conventional farming systems could enhance the contribution of agrobiodiversity (*e.g.* carabid beetles) and related ecological functions to cereal production.

These results are consistent with existing literature: while limiting the nutrient deficit and pest infestation of crops, mineral fertilisation and pesticides lessen carabid and plant diversity, as well as aphid and weed predation potential (Emmerson et al., 2016; Geiger et al., 2010;

Table 2
Summarised results of the Partial Least Square Path Models (PLS-PM). Results show path coefficients (Estimates) and their significance as tested by t-tests in the linear models and by bootstrap (B = 200). Significant results (p-value < 0.05) are in bold. Depending on the selected manifest variables, latent variables may have different interpretation between the two study years (see Fig. 2 for list of selected MVs).

	2016					2017				
	Linear model			Bootstrap		Linear model			Bootstrap	
Path	Estimate	p-value		perc.025	perc.975	Estimate	p-value		perc.025	perc.975
Farming Intensity -> Local-field agrobiodiversity	**-0.44**	**0.026**	*	**-0.776**	**-0.032**	-0.06	0.724		-0.330	0.301
Farming Intensity -> Pollination potential	**-0.50**	**0.027**	*	-0.944	0.142	0.09	0.662		-0.348	0.471
Farming Intensity -> Pest control potential	-0.15	0.549		-0.555	0.480	-0.19	0.346		-0.501	0.237
Farming Intensity -> Cereal production	**0.86**	**< 0.001**	***	**0.256**	**1.353**	0.03	0.832		-0.228	0.351
Local-field agrobiodiversity -> Pollination potential	**-0.54**	**0.025**	*	**-1.047**	**-0.005**	**-0.54**	**0.024**	*	-0.939	0.120
Local-field agrobiodiversity -> Pest control potential	0.10	0.707		-0.537	0.860	0.04	0.854		-0.518	0.561
Local-field agrobiodiversity -> Cereal production	**0.64**	**0.010**	**	-0.389	1.169	-0.20	0.312		-0.611	0.221
Pollination potential -> Cereal production	**0.44**	**0.040**	*	-0.299	0.855	-0.18	0.268		-0.517	0.110
Pest control potential -> Cereal production	0.29	0.098	.	-0.316	0.719	0.15	0.362		-0.202	0.465
Land. hetero. SNC -> Local-field agrobiodiversity	0.38	0.063	.	-0.308	0.858	**0.44**	**0.015**	*	-0.283	0.664
Land. hetero. SNC -> Pollination potential	-0.14	0.515		-0.482	0.267	0.40	0.073	.	-0.034	0.747
Land. hetero. SNC -> Pest control potential	-0.09	0.721		-0.627	0.599	-0.10	0.627		-0.523	0.326
Land. hetero. SNC -> Cereal production	-0.16	0.380		-0.614	0.297	**-0.60**	**0.003**	**	**-1.066**	**-0.176**
Land. hetero. crop mosaic -> Local-field agrobiodiversity	**0.47**	**0.028**	*	-0.235	0.866	0.29	0.103		**0.029**	**0.505**
Land. hetero. crop mosaic -> Pollination potential	0.36	0.125		-0.400	0.923	-0.01	0.980		-0.412	0.451
Land. hetero. crop mosaic -> Pest control potential	0.23	0.404		-0.447	0.747	0.40	0.063	.	-0.113	0.749
Land. hetero. crop mosaic -> Cereal production	-0.20	0.353		-0.791	0.489	0.22	0.222		-0.126	0.686

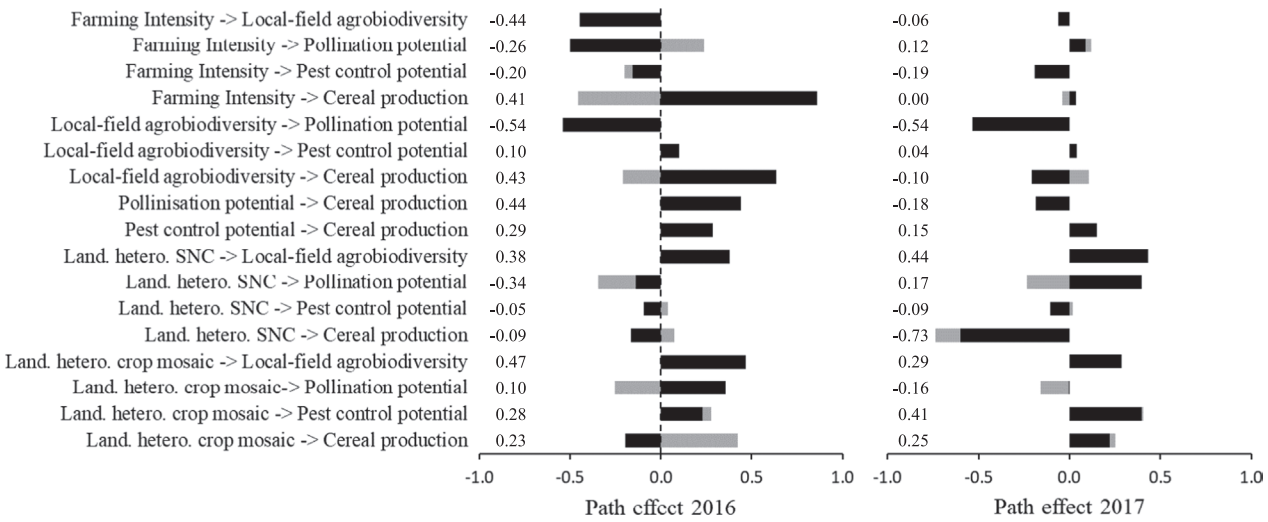


Fig. 3. Direct (black) and indirect (grey) path effects of independent latent variables (LVs) on dependant LVs for the Partial Least Square Path Models (PLS-PM) presented in Fig. 2. Values indicate the net effect (direct + indirect). Depending on the selected manifest variables, latent variables may have different interpretation between the two study years (see Fig. 2 for list of selected MVs).

Trichard et al., 2013). Bees are also strongly impacted by farming intensity through direct lethal, and sub-lethal (behavioural) effects of insecticides (Brittain and Potts, 2011), but also herbicides that reduce flower availability (Bretagnolle and Gaba, 2015; Carrié et al., 2018), with consequences on pollination (Kremen et al., 2002). However, the positive effect of pollination potential on cereal production may be surprising here as we studied non-entomophilous crops (wheat, triticale, and barley). One potential reason is that some pollinators, such as hoverflies, are also natural predators of pests (*e.g.* aphids) at larval stage (Raymond et al., 2014). Our study follows the agroecological framework where ecological functions associated with mobile organisms (such as pollinators) depend on the dynamic of the entire landscape mosaic (in terms of composition, configuration, and management practices, Vialatte et al., 2019). Therefore, pollination may correlate with a generally high abundance of beneficial species and good agroecosystem functioning, which makes pollination measures indicators of other important ecological functions (IPBES, 2016). This assumption is supported by the fact that in absence of these relationships (as tested in the first alternative conceptual model, Appendix S2), the model explained a lower proportion of observed variation.

4.2. Agrobiodiversity and farming intensity had comparable net effect on cereal production

The contribution of local-field agrobiodiversity, and particularly of the carabid beetle community, to cereal production was crucial. Its net positive effect was as high as the net effect of farming intensity (Fig. 3). However, we found negative and non-significant influence of our measures of local-field agrobiodiversity (representing carabids community) on pollination and pest control potential respectively (similar results was found in 2017). A potential reason for the absence of positive effect is that our measures were made 50 m away from field edges, where such relationships are expected to be highest as a result of spill-over. Our result on the negative influence of local-field agrobiodiversity on pollination potential was unexpected. This result may reflect an antagonism between carabid diversity (which was selected in the PLS-PM model) and pollinator communities, with, for example, contrasted responses to landscape context and/or interactions with weed communities (some carabids being seedeaters, Petit et al., 2018). In that sense, our results highlight the difficulty to use comprehensive and representative indicators of agrobiodiversity and ecological functions in agroecological studies. For instance, frozen preys, glued on predation cards, are useful but imperfect surrogate for actual pest control (*e.g.* omitting parasitism). The role of agrobiodiversity in providing pest control has been controversial for a long time. Ricketts et al. (2016), in a meta-analysis, have shown that more than half of studies linking biodiversity and pest control have not demonstrated any significant relationship. However, opposite to our results, a recent global data synthesis showed that diversity of beneficial communities (richness rather than abundance) support pollination and pest control, which in turn increases crop production (Dainese et al., 2019).

Nevertheless, local-field agrobiodiversity (carabid community) had a direct positive effect on cereal production. This relationship may not be interpreted as a causal relation but could reflect a positive correlation between agrobiodiversity and ecological functions not, or only partially, measured here (Table 1). For instance, carabid beetles are good indicators of soil characteristics, biodiversity, and related ecological functions, which were missing herein (Koivula, 2011). Future research should include the soil components of agroecosystems, as they were found to interact with farming intensity and ecological functions (Bartomeus et al., 2015; Gagic et al., 2017).

4.3. Landscape heterogeneity enhanced agrobiodiversity and ecological functions

While farming intensity had negative effects on agrobiodiversity and ecological functions, landscape heterogeneity had positive effects in both years (Fig. 2). In 2016, heterogeneity of the crop mosaic (primarily crop diversity), had a stronger positive effect on local-field agrobiodiversity (carabid beetle community) compared to semi-natural covers. Similarly, Sirami et al. (2019) found in an extensive study that increasing crop heterogeneity was more beneficial for multitrophic diversity of crop field communities than increasing semi-natural covers. While they found that smaller field size (*i.e.* higher edges density) was more important compared to crop diversity, we observed the opposite trend, perhaps because of different study gradients or response variable. These relationships lead, in our study, to an indirect positive effect of crop mosaic heterogeneity on cereal production (Fig. 3).

Similarly to Martin et al. (2020), we found that the positive effect of landscape heterogeneity on agrobiodiversity was similar or even larger than the negative effect of farming intensity (Table 2). Recent studies suggest that the effect of landscape heterogeneity on agrobiodiversity,

ecological functions and cereal production may be even greater when local farming intensity is lower (an interaction not studied here because of a too small sample size). For instance, Ricci et al. (2019) showed that an increased amount of semi-natural covers benefited biological pest control only at a low field-level pesticide use. Such interaction was also found at the landscape level, where the positive effect of landscape complexity on bee species richness occurred in landscapes with low nitrogen inputs (Carrié et al., 2017). These results call for investigations that quantify the potential of agroecological systems, when low-input farming practices are applied at the landscape-scale.

4.4. Annual variability of observed patterns

Our results strongly differ between the two years of measurements, with most relationships observed in 2016 collapsing in 2017 (Fig. 2). A potential reason is that 2017 was marked by drought and local storm events in the spring, as compared to 2016 (see method section). Weather conditions have been shown to be the main drivers of variations in ecological processes such as pest outbreak risk (Delaune et al., 2021). However, it is not possible to infer the respective influence of weather and stochastic variability based on a two-year study. Observed variations in yield, agrobiodiversity, and levels of ecological functions between 2016 and 2017 may have also resulted from other factors such as field history, as sampled fields differed between the two years. Non-measured local characteristics such as soil quality (texture, organic matter content) and soil biodiversity may have generated variations among study fields as well (Bartomeus et al., 2015; El Mujtar et al., 2019).

Nevertheless, our result suggests that neither increased farming intensity (particularly of herbicide use) nor ecological functions could compensate for the decline in crop production in 2017. However, persistence, or stability, across years of ecological communities and associated functions is critical for agroecological systems and stable crop production. Spillover of beneficial species into crop fields from semi-natural habitats is recognised to be critical for mitigating the negative effects of global environmental change on biodiversity patterns and ecological processes (Tscharntke et al., 2012). Landscape heterogeneity, particularly the amount of semi-natural covers (Fig. 2b), significantly increased local-field agrobiodiversity in 2017 (representing both plant and carabid communities). This effect was still too weak to maintain ecological functions and cereal production.

Stronger resilience to unfavourable factors, such as meteorological conditions, might however be provided by drastic modifications in farming systems such as less intense soil management (*e.g.* no tillage and direct seeding), longer crop rotations, intercropping, remaining previous crop residues or crop mixing (Duru et al., 2015). For instance, organic farming was found to support spatiotemporal stability of bumble bee and butterfly communities (Carrié et al., 2018). If such agroecological practices are implemented, in combination with increased landscape heterogeneity, it may be possible to increase the levels of biodiversity in crop fields and its contribution to cereal production, along with persistence of important ecological functions. In a national-scale study in the UK, Redhead et al. (2020) found that wheat crop yield was more stable and more resistant to extreme weather events in landscape with larger area and less fragmented semi-natural covers. Since the frequency of extreme meteorological events is likely to increase dramatically under climate change, research should urgently explore how landscape agroecological approaches can improve the resilience of agroecosystems.

5. Conclusion

In addition to the well-known environmental and public health issues associated with conventional farming practices, our results illustrate their limits for crop production itself. We found a high contribution of agrobiodiversity to crop production, even under the constraints from conventional farming practices. Active management aiming to increase the intensity and impact of ecological functions on agricultural production should combine a reduction of farming intensity and an increase of landscape heterogeneity. Specifically, we confirm that increasing heterogeneity of the crop mosaic (crop diversity and reduced field size) can be effective in maintaining biodiversity and ecological functions that contribute to crop production, without taking land out of production (Fahrig et al., 2015; Martin et al., 2020; Sirami et al., 2019).

Evaluating indirect effects through path modelling approaches (such as PLS-PM or Structural Equation Model) is a powerful tool for agroecological research, as shown by previous studies (Dainese et al., 2019; Gagic et al., 2017; Puech et al., 2015; Quinio et al., 2017). Further studies should include the soil component of the agroecosystem as it may have an important role as a productive factor, influencing important ecological functions, and for resilience to unfavourable meteorological conditions (water storage and absorption).

Our results raise questions on how much farmers are aware of the indirect negative influences their farming practices may have on agroecosystems and ultimately on yields. The net contribution of agrochemicals on crop yield remains positive, but this may not be sustainable in the long-term. Farmers' perception is a critical issue, as for instance, landscapes with greatest wheat yields do not have the highest yield stability or resistance to extreme weather events (Redhead et al., 2020). Recognising the counter-productive effect of high farming intensity and its incapacity to provide stable agricultural production is certainly a major step to encourage the transition towards agroecological production systems.

Author contributions

AV devised the conceptual idea of the study; RD led the writing of the manuscript, RD and MSC conducted the statistical analyses; RD, AV and MSC wrote the manuscript; AV, DS and MF designed the experimental sampling. EA, JPC, DE, AO, JRM, CS, and AV collected field data; SL supervised GIS data and performed GIS analyses. All co-authors made a significant contribution to the final manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendices S1 and S2. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107810.

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