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Alienor Jeliazkov*[ab1], Anne Mimet[ab], Rémi Chargé[c], Frédéric Jiguet[a], Vincent Devictor[d] & François Chiron[e]

[a]Centre d'Ecologie et de Sciences de la Conservation (CESCO), UMR 7204, Muséum National d'Histoire Naturelle, Sorbonne Universités, MNHN, CNRS, UPMC, CP51, 55 rue Buffon, 75005 Paris, France

[b]Laboratoire Dynamiques Sociales et Recomposition des Espaces (Ladyss), UMR 7533, CNRS, Université Paris 1 Panthéon-Sorbonne, 2 rue Valette, 75005 Paris, France

[c]Centre of Excellence in Biological Interactions, Department of Biological and Environmental Science, P.O. Box 35, 40014 University of Jyväskylä, Finland

[d]Institut des Sciences de l'Evolution, UMR 5554 CNRS-UM2, Université Montpellier 2, Place Eugène Bataillon, 34095 Montpellier cedex 05, France

[e]Laboratoire Ecologie, Systématique et Evolution, UMR 8079, AgroParisTech, CNRS & Université Paris Sud Orsay, France

[1][Present address] Laboratoire Dynamiques Sociales et Recomposition des Espaces, UMR 7533, CNRS, Université Paris 1 Panthéon-Sorbonne, 2 rue Valette, 75005 Paris, France

*****Corresponding author: Alienor Jeliazkov
alienor.jeliazkov@gmail.com
Phone number: +33(0)1 44 07 76 11

Abstract

Following the multiplicity of studies dealing with the effects of agricultural intensification on bird diversity, one of the lessons drawn is that these effects depend on both the taxonomic group, the component of diversity, the aspect of intensification, and the spatial scale. This often leads to disparate results among studies suggesting that the investigation of agriculture-biodiversity relationships suffers from scale-dependence, information redundancy, non-linearity problems, and thus, unpredictability.

Here, we propose a multi-scale and multi-facet approach to clarify the impacts of agricultural intensification on biodiversity and possible mitigating actions. Our study is based on bird and agricultural practice surveys of 199 agricultural fields in three agricultural regions of France. Using landscape characteristics and agricultural practice variables, we disentangled four main gradients of agricultural intensification on our study sites: landscape opening (farmland expansion), landscape homogenisation (decrease in crop and land cover diversity), chemical intensification (fertiliser, insecticide, and fungicide), and tillage *vs*. herbicide.

We tested whether and how these gradients interacted with each other at field, farm and regional levels in shaping taxonomic diversity (alpha, gamma and beta diversity) and ecological responses of bird communities (relative proportion of specialist *vs*. generalist species, trophic categories).

Landscape homogenisation and opening affected the taxonomic and ecological responses of birds at field and farm levels, but not at the regional level, highlighting the scale-dependence of agriculture-biodiversity relationships. At field and farm levels, landscape opening had a positive effect on beta diversity, and community specialisation by enabling the existence of farmland specialists, while heterogeneous landscapes promoted generalists.

Chemical intensification had negative impacts, especially at the farm level and on almost all facets of diversity. However, some bird species seemed to tolerate higher levels of both chemical and tillage intensification.

Some important interaction effects between landscape and agricultural practices, which are often disregarded, were also revealed, such that landscape homogenisation in interaction with tillage reduction was correlated with higher specialisation.

The field level appeared mostly relevant for explaining community variations by habitat and resource availability. Meanwhile at the coarsest scale, i.e. the Small Agricultural Region, only some possible dispersal limitations were likely to occur. Finally, our results highlight the farm level (intermediate scale) as a relevant unit for management and agricultural policies, since the community responded to both landscape and agricultural practices intensification at this

level. In particular, we emphasize the necessity to conserve both heterogeneous and homogeneous agricultural landscapes under extensive practices; the former promotes taxonomic diversity, when the latter favours specialised farmland biodiversity.

Keywords: Farmland bird diversity; Landscape homogenisation; Crop practices; Agricultural intensification; Scales; Species traits

Highlights

- Multi-scale impacts of Agricultural Intensification on farmland bird biodiversity?
- Taxonomic diversity is affected by landscape simplification at field & farm scales.
- Taxonomic diversity is affected by chemical intensification at farm scale.
- Specialisation & trophic complexity influence taxonomic responses to AI.
- Landscape and practices interactions mitigate biodiversity responses to AI.

1. Introduction

Agricultural intensification has multiple detrimental impacts on biodiversity caused by the degradation of suitable habitats (Altieri, 1999) and a reduced availability of resources (Benton et al., 2003), especially for farmland birds (Donald et al., 2001).

The effects of agriculture intensification through landscape modifications on biodiversity have been widely studied those last decades (Tscharntke et al., 2005). As a result, several conceptual compromises of land management have been proposed (e.g. Wildlife friendly farming *vs.* land sparing; (Fischer et al., 2008; Green et al., 2005) in order to conciliate crop production and biodiversity conservation. Most of these compromises give rise to important scale issues among others (Gonthier et al., 2014; Phalan et al., 2011; Quinn et al., 2012) because, to find optimal spatial scales of managing, one needs to understand at which scales biodiversity responds to environmental conditions.

The intensification of agriculture through intensive field practices and habitat simplification has been shown to influence bird biodiversity at the field, farm, landscape and/or regional levels (Gabriel et al., 2010). For instance, higher pesticide and fertiliser inputs and loss of semi-natural habitats reduce bird richness at the field and regional levels because of the extirpation of farmland specialists (Filippi-Codaccioni et al., 2010; Karp et al., 2012; Tscharntke et al., 2008). Agricultural intensification can also affect functional diversity but not necessarily in the same direction as taxonomic diversity, depending on the spatial scale considered (Devictor et al., 2010; Filippi-Codaccioni et al., 2010; Meynard et al., 2011). Overall, ignoring the multi-facets of biodiversity and the scale dependency in individual responses to agricultural intensification may lead to a simplistic view of biodiversity dynamics in farmlands and jeopardises the specific conservation efforts that should be implemented (Clough et al., 2007; Gabriel et al., 2010; Hendrickx et al., 2007). Moreover, although the potential interaction effects on biodiversity between landscape modifications and agricultural practices intensification have been suggested, they are still poorly quantified across scales that may be relevant in terms of land management (e.g. field, farm, agricultural region).

Partitioning diversity into local (namely alpha), inter-local (namely beta) and regional (namely gamma) diversities (Whittaker, 1972) offers a view of multi-scale agriculture-biodiversity relationships (e.g. Flohre et al., 2011; Gabriel et al., 2006). However, this partition (additive or multiplicative) has been weakened by many methodological limitations, notably the non-independence between real turnover and change in species richness (De Bello et al., 2010; Jost, 2007; Karp et al., 2012; see also Appendix A), and the inability to disentangle species-specific differences among sites (Jurasinski et al., 2008).

To remedy these limitations, firstly, we used a measure of beta diversity which was calculated independently to alpha, i.e. as a measure of inter-sites dissimilarities which will allow drawing hypothesis on species-specific contributions to the general patterns of beta diversity. Secondly, according to Baselga (2010), we proposed to partition beta diversity into

two independent components: nestedness and spatial turnover. Nestedness refers to community size (i.e. species richness) and occurs when all species belonging to smaller communities also belong to richer communities (see Wright and Reeves, 1992). A beta diversity which is only determined by nestedness thus results from differences in community size, reflecting a non-random process of species loss (or gain) as a consequence of any differences in habitat suitability, occupancy level (Gaston and Blackburn, 2008), and selective colonization or extinction (Cook and Quinn, 1995). True spatial turnover occurs regardless of the difference in community size and results from the replacement of some species by others, due to environmental filtering or spatial and historical constraints. Defining beta diversity as nestedness and spatial turnover allows disentangling and testing alternative hypotheses on the processes structuring diversity, regardless the inventory diversity (Jurasinski et al., 2008).

Complementing the information derived from taxonomic diversity indices, several integrative indices have also been proposed to quantify the relative abundance of species with specific traits that can shape diversity patterns.

Indeed, for instance, the preference for the farmland habitat strongly contributes to the species positive response to landscape homogenisation (Clavero and Brotons, 2010; Guerrero et al., 2011). Thus the Species and the Community habitat Specialisation Indices (SSI and CSI, respectively) were shown to decrease with habitat disturbance and fragmentation in farmland (Devictor et al., 2008; Filippi-Codaccioni et al., 2010). Specialisation of farmland communities is also favoured by low-intensity practices (Doxa et al., 2010). Similarly, a Community Trophic Index (CTI), adapted from the Marine Trophic Index (Pauly and Watson, 2005), has been proposed as a surrogate of the potential trophic complexity within bird communities (Jiguet et al., 2012). This index has not yet been tested in agricultural landscapes, though these have been shown to favour granivorous and ground insectivorous species, leading to less diversified diet composition in farmland than in forested areas (Hanspach et al., 2011).

Agriculture intensification is characterized by high levels of chemical inputs (pesticides and fertilizers), tillage operations and landscape homogenisation (or simplification) (e.g. Flohre et al., 2011; Wilson et al., 1999). Landscape homogenisation is usually described based on two features: land use intensification (Flynn et al., 2009) and agriculture expansion (Medan et al., 2011). At the local scale, land use intensification relates to the intensity of agricultural practices (Flynn et al., 2009), while at the landscape scale, it is strongly related to agriculture expansion (Tscharntke et al., 2005). Indeed, a landscape is intensively managed when entirely agricultural and less intensively managed when composed of half-agriculture half-natural, or semi-natural land covers. Thus, in this study, we integrated these different aspects of agricultural intensification; landscape alterations, as represented by land use intensification and agriculture expansion, and practices intensification.

We aimed to disentangle the changes in bird taxonomic diversity and in specialisation and trophic complexity due to landscape characteristics and agricultural practices at different

spatial scales. For this purpose, we investigated the responses of alpha, beta and gamma diversities, and ecological indices (CSI, CTI) of the community to landscape characteristics and agricultural practices, using a bird survey conducted on 199 fields in three French agricultural regions in 2010 and 2011. Then, we analysed the species-specific contributions to the observed changes in beta diversity in order to relate the changes in community composition and spatial distribution of species to particular ecological traits. This provided an interesting opportunity to complement the community approach with a focus on species for a better understanding of the biodiversity responses to environmental gradients in agricultural landscapes. In particular, we focused on the following predictions.

(i) We expected negative effects of agricultural intensification on bird diversity, resulting from habitat homogenisation across spatial scales (Pickett and Siriwardena, 2011), and from increased use of pesticides (through toxicological poisoning or by resource depletion; (Boatman et al., 2004; Mitra et al., 2011). A homogenisation of the communities (decrease of beta diversity) was expected at farm and regional levels but not necessarily at the field level, this latter being more prone to environmental heterogeneity than the two others (Flohre et al., 2011; Karp et al., 2012). We further aimed at explaining this scale-dependence of beta diversity by differences in species ecological traits.

ii) Moreover, we expected mixed effects of agricultural practices and landscape structure on biodiversity (Geiger et al., 2010; Quinn et al., 2012; Rundlof and Smith, 2006; Wretenberg et al., 2010), especially through interactions between farming strategies or crop types and landscape composition. For instance, in croplands, depending on the taxonomic and functional group, Agri-Environment Schemes or even hedges and organic farming seem more effective in enhancing species richness in simple than in complex landscapes (Batáry et al., 2011, 2010). Some interaction effects between agricultural expansion and level of practice intensification have been shown on alpha and beta diversity of birds (Flohre et al., 2011), but what species are involved in this responses are unknown. Moreover, interaction effects, when tested, were based on contrasting sampling conditions, thus necessarily on an arbitrary and dichotomous approach of agricultural intensification (Tscharntke et al., 2012a). However, how *gradients* of landscape structure in terms of composition and diversity (McGarigal and Cushman, 2005) interact with gradients of agricultural practices, i.e. according to different chemical and tillage pressures, is still unclear and was not quantified. Thus, we predicted that more diverse and heterogeneous landscapes could mitigate the negative impacts of intensive agricultural practices.

(iii) At species level, farmland specialists have been shown to have suffered declines in Europe over the last twenty years attributed to agricultural intensification (Donald et al., 2001; Guerrero et al., 2011; Vickery et al., 2004). The sensitivity to agricultural intensification greatly varies from a species to another (Bengtsson et al., 2005; Quinn et al., 2012). Given that some species with specific traits are more at risk than others in terms of abundances (Pickett and Siriwardena, 2011), we expected these species to contribute more to the local change in diversity along agricultural gradients.

In particular, we expected the diet complexity, and the specialisation, to play a part in the sensitivity of farmland species to agricultural intensification, as these traits are involved in resource foraging, and in suitable habitat seeking, respectively. Tillage and pesticide use and landscape homogenisation (Hanspach et al., 2011) were expected to disfavour ground feeders (by resource decrease), narrowing the diet complexity in farmland communities, and consequently, the species richness.

2. Materials and methods

2.1. Study sites and sampling design

Study sites were selected in three French departments in which the proportion of cereal crops is representative of the cropping regions of northern France (crop cover >= 25% of the overall territory): Aisne, Yonne and Charente-Maritime (Fig. 1, see Appendix A).

The study followed a nested design where fields constituted the smallest spatial level (Fig. 1e) and were contained within blocks (Fig. 1b-e). The blocks were themselves distributed among eight different Small Agriculture Regions (SARs) located in three departments (Fig. 1b-d). The SAR level is a French zoning system of units with homogeneous agricultural systems, soil and climate (Klatzmann, 1955). Blocks were located in municipalities that contained more than 25% of arable land, according to the CORINE Land Cover database (CLC 2006, level 2; EEA-ETC/SIA, 2007). Blocks consisted of four to five cereal fields (maize excluded) and covered an area of approximately 2*2 km, which is close, in order of magnitude, to a farm level in open field areas. In order to optimise cross-scale representativeness of the whole landscape while keeping a reasonable landscape variability, the blocks and fields were selected (i) provided that their surrounding landscape presented a crop cover proportion higher than 60% (in a 1500-m-radius buffer area) and 30% (in a 300-m-radius buffer area, Fig. 1) respectively, and (ii) avoiding urban areas in the direct vicinity. In total, 199 fields and 39 blocks were studied, including 107 fields in 2010 and 92 additional fields in 2011. The fields belong to 42 farmers who gave us their permission to conduct the study on their cereal fields and described their practices on these fields.

2.2. Landscape characteristics, agricultural practice data, and gradients of agricultural intensification

Landscape characterisation

CORINE Land Cover (level 3) was used to characterise the composition and diversity of the main land cover types (13 in total, including e.g. woodlands, permanent crops, arable lands, grasslands, etc.). The French Registre Parcellaire Graphique database (RPG, 2008, Agence de

Services et de Paiement, Ministère de l'Agriculture, www.geoportail.fr) was used to characterise the diversity of crop types (28 in total, including e.g. wheat, barley, maize, rape, grasslands, protein crops, vineyards, etc.), and the area of surveyed fields. These databases were processed using the GIS tool Quantum GIS 1.7.4 (www.qgis.org) to extract five variables describing the surrounding landscape of fields and blocks: the relative proportions of cultivated/arable and woodland areas, the field area, and the landscape diversities of land cover types and of crop types. Both the variables of diversity of land types and of crop types were based on the Shannon's diversity index (McGarigal and Marks, 1995) calculated as following:

$Sh_{land;crop} = -\sum_{i=1}^{m}(P_i \times ln\, P_i)$where $Sh_{land;crop}$ is the Shannon's diversity index representing the diversity of land or crop types, respectively, i the type of land or crop, m the total number of land or crop types, and P_i the proportion of the surrounding area occupied by the ith type of land or crop, relatively to the area occupied by the total number of m types of land or crop, respectively.

At the block level, the landscape variables were calculated within a 1500-m-radius buffer centred on the centroid between the four or five fields constituting the block. At the field level, the variables calculated in two 300-m-radius buffers centred on the bird count points were averaged (Fig. 1e).

Agricultural practices

A standardised survey was conducted among the 42 crop farmers about their agricultural practices between 2009 and 2011 (Appendix B). Information regarding soil preparation and the use of herbicides, fungicides, insecticides and fertilisers was collected. Based on these data, five practice variables were computed at the field level and throughout the period of the survey: tillage index (coded such as: 1=conservation tillage, i.e. shallow tillage, simplified cultivation techniques, *vs.*2=full tillage), and the mean annual number of herbicide, fungicide, insecticide and fertiliser applications. These variables were then averaged at the block level.

Determination of gradients of agricultural intensification by PCA

Agricultural intensification was summarized by conducting two Principal Component Analyses per level (field and block) (PCA, R package {ade4}; Dray and Dufour, 2007) on the five landscape variables to describe landscape simplification and on the five practice variables to reflect agricultural practice intensification.

2.3. Bird survey and taxonomic and ecological responses of the community

Bird survey

A standardised protocol adapted from the French Breeding Bird Survey was used to monitor bird species in each field (Julliard and Jiguet, 2002). Birds were surveyed at two count points per field, located along the field margin and spaced by at least 250 m to avoid double counting (Fig. 1e). Count points were monitored twice in each spring of 2010 and/or 2011, once before and once after 8th May, with 4-6 weeks between the two counting events. Every bird species heard or seen during a 5-min period within the field or in the surrounding area (100-m-radius around the observer) was recorded. Bird counts were carried out by four experienced birders, in the morning from dawn to midday at the latest, under suitable weather conditions; 76 species were retained (Appendix C). The maximum number of individuals across the visits during the two years was recorded. These abundances were then summed across the two count points in order to get a proxy for the relative abundance of each species at the field level (in accordance with the protocol of the French Breeding Bird Survey after Jiguet et al. (2012)).

Taxonomic responses of the community: alpha, beta and gamma diversities

To investigate the responses of bird taxonomic diversity across spatial levels, the Shannon's diversity index was calculated at field (Sh_{field}) and block (Sh_{block}) levels (averaged over 2010 and 2011), representing alpha and gamma diversities, respectively, as following:

$$Sh_{field;block} = -\sum_{i=1}^{N}(a_i \times ln\ a_i)$$

where $Sh_{field;block}$ is the Shannon's index diversity of birds at field or block level, respectively, i the species, N the total number of species, and a_i the abundance of the ith species relatively to the total number of species, at field or block level, respectively.

To assess total beta diversity, the Jaccard dissimilarities index (*JacTOT*) was used. Following Baselga's method, the beta diversity was further partitioned into its turnover (*JacTU*) and nestedness (*JacNE*) components (Baselga, 2010). Thus, the inter-field beta diversity (i.e. the beta diversity between fields within blocks) and the inter-block beta diversity (i.e. the beta diversity between blocks within SARs) were computed and partitioned. Calculations for alpha and gamma, and beta diversities were processed with R 2.15.3 (R. Core Team, 2014) with the packages {vegan} (Oksanen et al., 2013), and {betapart} (Baselga et al., 2013), respectively.

Ecological responses of the community: CSI and CTI

The Species Specialisation Index (SSI) is the coefficient of variation of one species' density across habitat types, and thus represents the habitat specialisation of that species (Julliard et

al., 2006). The Species Trophic Index (STI) represents the position of one species within a trophic network according to three categories: granivorous, insectivorous and carnivorous (Jiguet et al., 2012). It is calculated as the weighted mean of the three diet proportions (plants, invertebrates and vertebrates) of birds, with a higher weight for higher trophic categories (see Princé and Jiguet, 2013). Both SSI and STI indices were calculated from the national database of the French Breeding Bird Survey (Julliard and Jiguet, 2002) by Julliard et al. (2006), and Jiguet et al. (2012), respectively.

To assess the ecological characteristics of communities, the Community Specialisation Index (CSI; Devictor et al., 2008) and the Community Trophic Index (CTI; Jiguet et al., 2012) were calculated at field and block levels. They result from the average abundance-weighted SSI and STI, respectively, and were calculated as follows:

$$CSI;CTI_{field;block} = \sum_{i=1}^{N} \frac{a_i \cdot SSI;STI_i}{a_{tot}}$$

where $CSI;CTI_{field;block}$ is the CSI or CTI, at the field or block level, i the species, N the total number of species, a_i the abundance of the species i, a_{tot} the total abundance of all N species, and $SSI;STI_i$ the SSI or STI of the species i.

Species-specific contribution to community distribution along farmland gradients

To elucidate the links between taxonomic patterns and ecological characteristics of the community, the contribution of four traits was tested (see next section for methodological details): Species Specialisation Index (*SSI*), Species Trophic Index (*STI*), percentage of species occurrence (*Occ. frequency*) as a surrogate information of distribution size (Davey et al., 2013) (calculated from our abundance data previously transformed into presences/absences), and species affinity with farmlands (*Status*). We attributed status farmland to species which abundance was higher in farmland habitats than in other habitats (i.e. more than 50% of its population), and status non-farmland to the other species. Proportion of each species abundance in farmland versus non-farmland habitats was calculated by using the French Breeding Bird Survey data (Jiguet, 2010, see Appendix A). See next section for methodological details.

2.4. Methods for analysing the agriculture-biodiversity relationships and their level-dependence

Each taxonomic (i.e. alpha/gamma diversities as Shannon's diversity index, and beta diversity as Jaccard dissimilarities) and ecological (i.e. Community Specialisation Index, Community Trophic Index) responses were modelled each separately as the dependent variables. The independent variables are the sites coordinates along the two axes derived

from the PCAs of landscape and agricultural practices variables (see Section 2.2), which refer to gradients of agricultural intensification.

Analysing the response of alpha/gamma diversities and of ecological indices to landscape and agricultural practice gradients To analyse the relationships between taxonomic and ecological responses (Shannon index, CSI, CTI) and the gradients of agricultural intensification (including interactions), Linear Mixed Modelling was used assuming a Gaussian response (R package {nlme}, Pinheiro et al., 2013). The random component of the mixed modelling allowed us to take into account the constraints due to the nested design and spatial dependence between the study sites. At field and block levels, a random effect was applied corresponding to block and SAR levels, respectively. As recommended by Zuur et al. (2009), the best random structure was assessed comparing the AIC scores of full models (i.e. with all fixed variables) fitted with the Restricted Maximum Likelihood method, which varied only by their random-effects structure.

Then, to determine the importance of fixed effects while limiting uncertainty from model selection, a model averaging procedure was applied (Wood, 2006) (R package {MuMIn}; Barton, 2013) on the models fitted with the Maximum Likelihood method (which allows comparing fixed-effects structure of mixed models based on their AIC, Zuur et al., 2009). All the possible models were ranked based on their AICc (corrected AIC for small sample size) and the best models were identified, i.e. the models with the smallest AICc in a range such that delta AICc < 4. The relative importance of each term (including interactions) was calculated as the sum of Akaïke weights over all of the models in which the term appears (Barton, 2013). In accordance with Viallefont et al. (2001), we considered a variable as noticeably important (and discussed it) when the resulting importance value (*Imp.*) equalled or exceeded 0.5, interpreted as a weak, positive, strong or very strong evidence if *Imp.* <0.75, <0.95, <0.99, or >=0.99, respectively (for the handling of multi-collinearity and spatial auto-correlation in our models, see Appendix A).

Analysing the response of beta diversity to landscape and agricultural practice gradients

To analyse the relationships between beta diversity components and environmental gradients (Tuomisto and Ruokolainen, 2006), Multiple Regressions were performed on distance Matrices (MRM; Legendre et al., 1994) (package {ecodist}; Goslee and Urban, 2007). A biological response matrix, i.e. here one matrix of Jaccard dissimilarities per level (i.e. block and SAR levels) was regressed against environmental matrices. The environmental matrices were based on the Euclidean distances between sites according to the values of their landscape and agricultural practice gradients, and their geographical position (see Appendix A).

The significance of the main and interaction effects of the environmental variables was assessed by a randomisation procedure on matrices (999 permutations) (Appendix A). The

variables showing p-values below the threshold of 0.05 were kept in the final model as dominant biodiversity drivers.

Assessing species-specific contributions to taxonomic responses

To analyse which and how species traits contributed to the patterns of beta diversity according to Davey et al.'s method (2013), a jackknife analysis was first applied to assess how individual species contributed to the modelled beta diversity. Each species was removed one by one from the dataset and beta diversity components were re-calculated. MRM analyses were then re-run and the partial coefficients of regression extracted. The relative species influence was calculated at both levels as follows:

$$SpInf_{block;SAR} = \sum_{p=1}^{N} \left[\frac{(C_{glob} - C_p)}{C_{glob}} \right]$$

where $SpInf_{block;SAR}$ is the relative species influence calculated for each species at the block or SAR level, p the significant parameter in the optimal model, N the total number of significant parameters in the optimal model, C_{glob} the value of the regression coefficient for the parameter p in the global model run on the complete pool of species, and C_p the value of the regression coefficient for the parameter p in the model run on the reduced pool of species, i.e. from which the focal species was removed.

To examine the relationships between the species contribution to beta diversity and species traits, a linear regression of the new variable *SpInf* against the four trait variables *SSI*, *STI*, *Occ. frequency* and *Status* was applied (see Appendix A).

3. Results

Of the 76 studied species, 21 were farmland specialists (Appendix C). The Shannon diversity of the community varied from 0 to 4.3, meaning that the community true diversity (i.e. the effective number of species, *sensu* Jost, 2006) varied from 1 to 74 species per field. The Community Specialisation Index was negatively correlated with Shannon diversity (field level: r = -0.66, df = 197, p < 0.001; block level: r = -0.81; df = 37, p < 0.001) and with the Community Trophic Index at the field level (r = -0.26, df = 197, p < 0.001), but not at the block level (r = 0.31, df = 37, p = 0.06) due to one singular block showing the lowest Shannon diversity (Sh_{Chouy} = 1.87, compared to a mean of 3.64 [SE = 0.12]).

3.1. Identification of four principal gradients of agricultural intensification

Interestingly, the PCAs computed separately on landscape and agricultural practice variables at field and block levels allowed us to identify four main independent components of agricultural intensification. These components are valuable because they are composed of

the equivalent variables at both field and block levels. All levels considered, the first two axes of the PCAs explained from 53% to 77% of the total inertia (Fig. 2):

Landscape simplification:

Farmland proportion increase: The first axis of the PCA on landscape variables corresponded (|r|>0.90) to the increase in crop cover and the decrease in woodlands in the landscape.

Landscape homogenisation: The second axis of the PCA on landscape variables represented (|r]>0.67) an increase in focal field areas, and a decrease in crop (and land cover) diversity in the landscape.

Agricultural practice intensification:

Chemical intensification: The first axis of the PCA on agricultural practice variables represented (|r|>0.53) an increase in fungicide, insecticide and fertiliser use.

Tillage *vs.* herbicide: The second axis of the PCA on agricultural practice variables corresponded (|r|>0.5) to an increase in herbicide loads opposed to a tillage intensification. As herbicide use and tillage largely share the function of destroying weeds, tillage reduction, often advocated as preserving soil life, lead to an increase in herbicide use.

Field and block scores for these principal components were used in the models as variables for the analyses at field and block levels, respectively.

3.2. Effects of agricultural intensification on bird diversities across spatial levels

Diversity responses to gradients of landscape simplification

The Shannon diversity index at both field and block levels (alpha and gamma diversities), decreased with farmland proportion increase and landscape homogenisation (Tables 1 and 2, and Fig. 3a-d). Differences between community compositions (i.e. total inter-field beta diversity) decreased with these two gradients of landscape simplification (Table 3).

In support of this result, community specialisation (CSI) increased with farmland proportion increase, and with landscape homogenisation, at both field and block levels (Tables 1 and 2, and Fig. 3e-h). At the field level, this relationship was even amplified by the marginal positive effect of the interaction between farmland proportion increase and landscape homogenisation (Fig. 4d).

The trophic index (CTI) was negatively linked with farmland proportion increase at the field level (Table 1). At the block level, the combined effects of farmland proportion increase and landscape homogenisation penalised high-trophic level categories (Table 2).

Diversity responses to gradients of agricultural practice intensification and interactions with landscape simplification

The response of diversity variables to chemical and tillage *vs*. herbicide intensification were level-dependent, as they were stronger at the block level than at the field level.

At the field level, the Shannon index (i.e. alpha diversity) was marginally (importance = 0.49 < 0.5) higher for two distinct combinations of agricultural practices, i.e. for a combination of high chemical intensification and low level of tillage, but also for a high level of tillage (low level of herbicide) and low level of chemical intensification (Table 1 and Fig. 4a), suggesting two different potential processes underlying the diversity patterns (discussed below). At the block level, the Shannon index (i.e. gamma diversity) decreased with chemical intensification and tillage reduction (and high herbicide use) (Fig. 4b-c). The turnover component of inter-field beta diversity increased when farmland proportion increased *simultaneously with* tillage reduction, meaning that tillage reduction enabled a replacement in the communities with species associated to more cropped landscapes (Table 3). The gradient of tillage reduction *vs*. herbicide intensification had important and complex effects on diversities; (i) it was related to two distinct but comparable patterns of diversity at the field level according to two contrasting combinations of tillage and herbicide use, (ii) herbicide use (extensive tillage) had a negative effect on Shannon's diversity at the block level, while (iii) extensive tillage had a positive effect on the species turnover between fields.

At field and block levels, community specialisation (CSI) was generally positively related to tillage reduction (Fig. 4e-g). At the field level, however, this positive response of the CSI to tillage reduction was true only in the context of farmland proportion increase, according to the notable importance of the interaction term between farmland proportion increase and tillage reduction (Table 1 and Fig. 4e). At the block level, the CSI was sensitive to the interaction between chemical and tillage intensification. A higher CSI was found for two cases: (i) low chemical use and low tillage, and (ii) high chemical and tillage intensification (specialists of highly open farmland) (Table 2 and Fig. 4g).

3.3. As for the community trophic index (CTI), high trophic-level categories were disadvantaged in open farmland and homogeneous and chemically intensive landscapes (Tables 1 and 2). **Species-specific contributions to beta diversity**

The results indicated that the inter-field total beta diversity was negatively correlated with farmland proportion increase and landscape homogenisation (Table 3). In particular, turnover and nestedness components were negatively and positively correlated to farmland proportion increase, respectively.

Generalized (*SSI*) farmland (*Status*) species were contributing positively to inter-field total beta diversity (according to the negative relationship between *JacTOT* and *SSI,* and *Status NF*, Table 4). The two components of beta diversity (turnover and nestedness) were both explained by *Occurrence frequency*. In particular, the turnover was also explained by farmland species (*Status*), thus common farmland species contributed to the increase of turnover.

At the inter-block level, the turnover component of beta diversity was explained only by spatial distances between blocks (Table 3), i.e. at equal species richness, the more the blocks are far from each other, the more the communities differ in terms of composition. There was a positive contribution of species' *Occurrence frequency* to this turnover component (Table 4).

4. Discussion

This study investigated whether and how the agricultural characteristics surrounding bird communities measured at multiple scales (field, farm and small agricultural region) influenced different responses of those communities (richness, diversity and ecological composition).

In accordance with previous studies, we found that landscape opening (farmland proportion increase), landscape homogenisation and intensive agricultural practices, both mechanical and chemical, were important factors in explaining bird diversity patterns and acted as environmental filters across multiple spatial levels, from local (i.e. fields) to intermediate (i.e. inter-field and block) and regional (i.e. inter-block) levels (Figure 5). While some of our results could have been derived from simpler studies focusing on one scale and one biodiversity facet, other results are clearly revealed by such a cross scale and multi-facet approach. For instance, this approach allowed us to disentangle two potential mechanisms underlying the distribution of bird diversity in response to agricultural intensification: the possible recruitment of farmland specialists at the local level in a context of landscape simplification which however may be hindered by the effect of agricultural practice intensification at coarser levels.

Our results bring new and complementary insights about the level-dependence of agriculture-biodiversity relationships, the importance of disentangling the effects of the different gradients of agricultural intensification, the interaction effects between landscape and agricultural practices, and the contribution of ecological characteristics to the patterns of taxonomic diversity in birds.

4.1. Importance of disentangling multiple gradients of agricultural intensification

In our study, agricultural intensification appeared to be multi-factorial, with each factor having particular effects on biodiversity responses. We identified four main independent gradients of agricultural intensification common to the three French departments studied. Two of these gradients were related to landscape simplification (landscape opening due to farmland proportion increase and landscape homogenisation), while the other two described agricultural practice intensification. In the context of farmland biodiversity decline, Europe funds are allocated to promote responsible agricultural practices *via* the Agri-Environment Schemes. Quantifying agricultural intensification is therefore necessary to

target and evaluate policies (Teillard d'Eyry, 2012). Our results point out that using a unique indicator of agricultural intensification restricted to either landscape characteristics, or pesticide use, may not be sufficient to evaluate and anticipate the complex effects of agricultural intensification on biodiversity. In particular, relating the changes in beta diversity to species-specific traits helps in understanding the ecological processes underlying the community distribution. This knowledge provides the bases upon which to conceive compromises of land management in agricultural areas.

4.2. Influence of agricultural intensification on taxonomic and ecological responses

At the regional level (Small Agricultural Region, i.e. inter-block level), bird diversity varied only with the distance between blocks; the further the blocks were from each other, the greater the dissimilarities between bird communities. Natural turnover of communities with geographical distance may reflect co-varying climatic changes (Monnet et al., 2014) between blocks and regions, or may be explained by different species dispersal or migration abilities between communities (Tuomisto and Ruokolainen, 2006). The latter process is supported here by the positive relationship between turnover and species occurrence frequency (proxy of the distribution area) at the regional level.

At intermediate and local levels (block and field), the decrease in taxonomic diversity was strongly related to agricultural intensification. Negative effects of farmland proportion increase and landscape homogenisation on bird diversity were consistent across spatial levels whereas environmental filtering due to agricultural practice intensification mainly operated at the block level. The decline in bird diversity in intensive agriculture is probably due to the simplification of the landscape and vegetation structure around cereal fields (Fischer et al., 2011). We highlighted the indirect effects of chemical and tillage practices on taxonomic biodiversity, probably resulting from the depletion of trophic resources, and nesting opportunities for farmland birds, especially ground nesters (Holland, 2004). These effects of agricultural practices specific to the block level which create an environment of poor quality at intermediate-scale, impact biodiversity more than isolated local practices.

Whether or not agricultural intensification causes declines in beta diversity by environmental (landscape and/or agricultural practice) homogenisation has been much debated (Flohre et al., 2011; Karp et al., 2012). We found that landscape opening and homogenisation had a clear negative effect on inter-field beta diversity: sites of similar habitat composition and structure had more similar species assemblages. Bird diversity erosion at the regional scale was mainly caused by a cumulative loss of diversity within blocks, and potentially by dispersal limitations between blocks. Other relevant information describing other components of biodiversity (e.g. taxonomic groups; Flohre et al., 2011; Gabriel et al., 2010) or farmland characteristics (e.g., the presence of field margins; Marshall

and Moonen, 2002; Vickery et al., 2009) might be needed to explain this region-wide biodiversity loss.

Overall, our results suggest that landscape homogenisation led to the selection of a pool of farmland birds that are specialised in open cropped habitats, as supported by the positive relationship between the inter-field turnover and farmland status of species. To a lesser extent, we showed that beta diversity was also driven by nestedness. This reflects the non-random loss of most widely distributed species, with the loss of species (selective extinction, Cook and Quinn, 1995) associated to landscapes composed by a mosaic of different habitats, and the gain of species (selective colonization) associated to more open and homogenised landscapes.

4.3. Explaining taxonomic responses by species' ecological traits

Similarly to other studies, the loss of taxonomic diversity under intensive agriculture was associated with a decrease in trophic complexity within bird communities (Ekroos et al., 2010; Tscharntke et al., 2008). In open and simplified landscapes, herbivorous and granivorous bird populations persisted better than insectivorous and carnivorous birds. A further decline in predatory species was observed when the use of insecticides and fungicides increased, probably reflecting poor (less diverse) and scarce resources. Moreover, the negative effects of landscape simplification and chemical intensification on trophic complexity amplified each other at field and block levels, indicating a non-linear effect of intensification, with a higher sensitivity of community to both gradients of intensification when combined. Overall, the diet of species might be a relevant trait to explain species assortment in intensive agriculture. However, the species trophic category (STI) was not involved in the beta diversity decline, suggesting that species replacement, and/or dissimilarities derived from nestedness, do not depend on the species position within the trophic network but maybe rather on the vegetation layer of foraging (Hanspach et al., 2011). By extension, all trophic levels can be affected by agricultural intensification. A thorough study of the biotic interactions would be necessary to test this hypothesis and draw further conclusions about the fine trophic mechanisms that potentially underlie these community patterns.

While trophic complexity decreased with farmland proportion increase, communities were composed of more farmland specialists (Fischer et al., 2011). As many of these are ground nesters, they are assumed to benefit from extensive soil preparation (conservation tillage *vs*. conventional) (Bas et al., 2009; Filippi-Codaccioni et al., 2009). Conservation tillage may have allowed invertebrate regeneration due to low soil disturbance, indirectly benefiting field-nesting and field-feeding birds. However, farmland specialists were negatively impacted by chemical intensification, as already shown by Fischer et al. (2011). Some specialist communities are thus enhanced in the context of extensive agriculture with low-frequency chemical use and reduced mechanical practices, but composed of wide open lands.

We found consistent responses of taxonomic and ecological responses to agricultural intensification across spatial levels. However, ecological response was more sensitive to interaction effects between landscapes and agricultural practices (mitigation or amplification effects), demonstrating the need to combine taxonomic and more ecological approaches and landscape and agricultural practice descriptions to better understand the biodiversity changes induced by agriculture.

5. Conclusions

Overall, we have shown the independent effects of landscape and agricultural practices induced by agricultural intensification on biodiversity. We have also revealed scale dependence in these biodiversity-agriculture relationships through three levels of study; field, farm and Small Agricultural Region, and we have explained the links between two facets of biodiversity; taxonomic and ecological.

Agricultural intensification decreased both alpha and turnover diversities of birds, predominantly within and between nearby farms. It operated through landscape simplification, i.e. homogenisation and opening due to farmland proportion increase. Communities were modified in size and composition with ecological consequences, as heterogeneous landscapes promoted a more generalist but also trophic-complex biodiversity. Thus, homogenised landscapes enabled the existence of farmland specialist communities, increasing diversity at the farm level and between farms. However, communities negatively responded to chemical and mechanical practices associated with agricultural intensification. These well-known patterns were however shown to be especially true at the farm level and to be obscured by interaction effects between landscape structure and specific agricultural practices. This was revealed thanks to a fine-scale and original description of the agricultural practices which are usually confounded in the description of the landscape, or classified according to coarse landscape-crop types associations. While changes in some agricultural practices may be relevant at the farm scale (e.g. the lower use of pesticides), other management actions should take place at the landscape scale (maintaining specific habitats for nesting of several species with different needs), allowing landscape complementation or supplementation (Tscharntke et al., 2012b).

Moreover, we explicitly tested the contribution of species with specific ecological traits, allowing a better understanding of the potential mechanisms at play.

From a conservation point of view, our results support the idea that the farm level represents a relevant unit of management for sustaining biodiversity. Preserving biodiversity and limiting biotic homogenisation in farmlands require the conservation of both heterogeneous landscapes to promote taxonomic diversity and open and homogenised landscapes to promote specialised biodiversity. In both cases, biodiversity conservation involves extensive agricultural practices to maintain biodiversity at scales equivalent to farms and beyond. These results resonate with previous studies showing that agricultural

policies need to be adapted according to the regional landscape (Quinn et al., 2012; Wretenberg et al., 2010). For instance, Geiger et al. (2010) and Batáry (2011) found that organic farming practices favour biodiversity only in simplified landscapes.

By extension, reducing farming intensity through moderated pesticide and mechanical use may increase bird biodiversity. This is typically the goal of integrated management systems, such as e.g. Good Farming Practices (Vickery et al., 2004). Quinn et al. (2012) suggested that while organic farming practices favour biodiversity, the benefits still need to be mitigated depending on the land management configuration across scales. In comparison, integrated systems, which currently cover a relatively high proportion of agricultural areas in France and in Europe compared to organic farming, could also contribute to farmland biodiversity conservation over a large scale.

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Figures

Figure 1

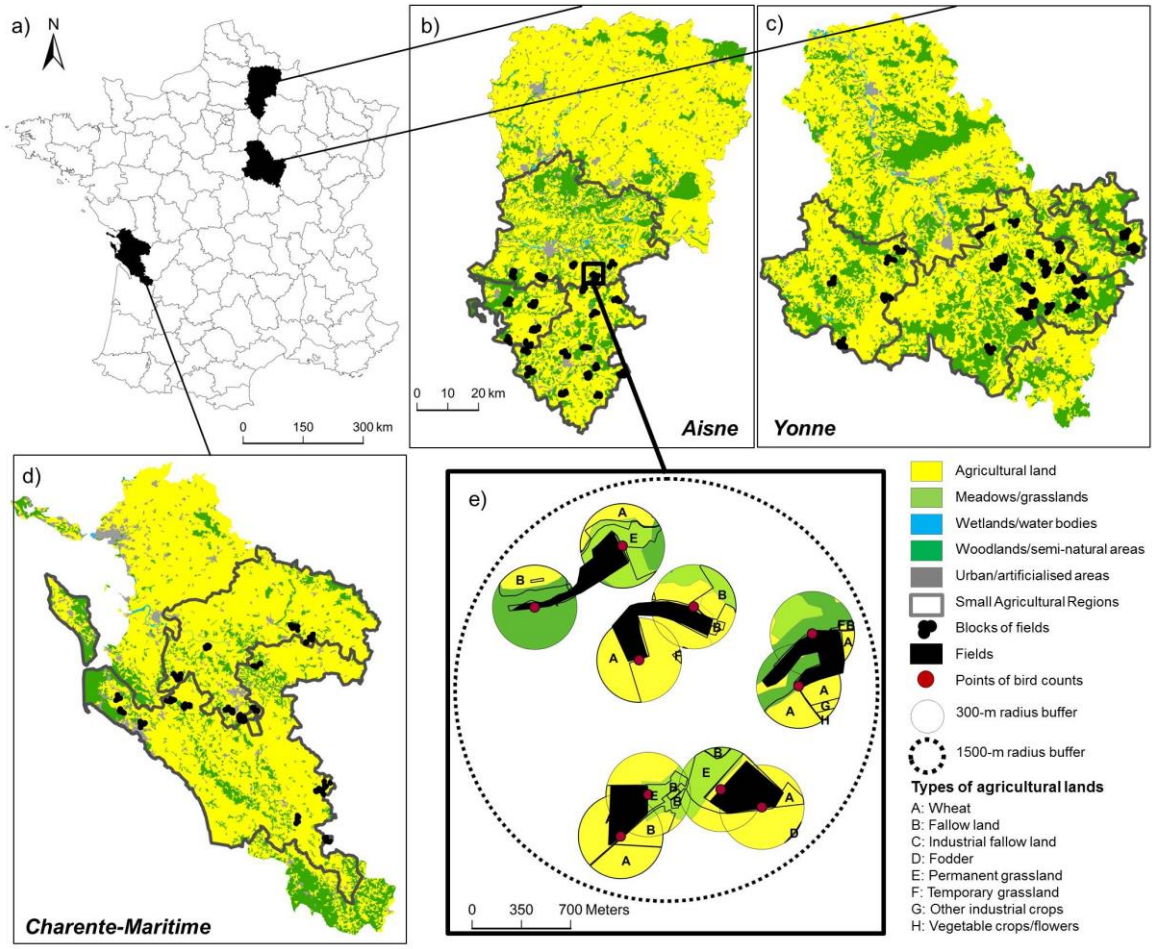

Figure 2

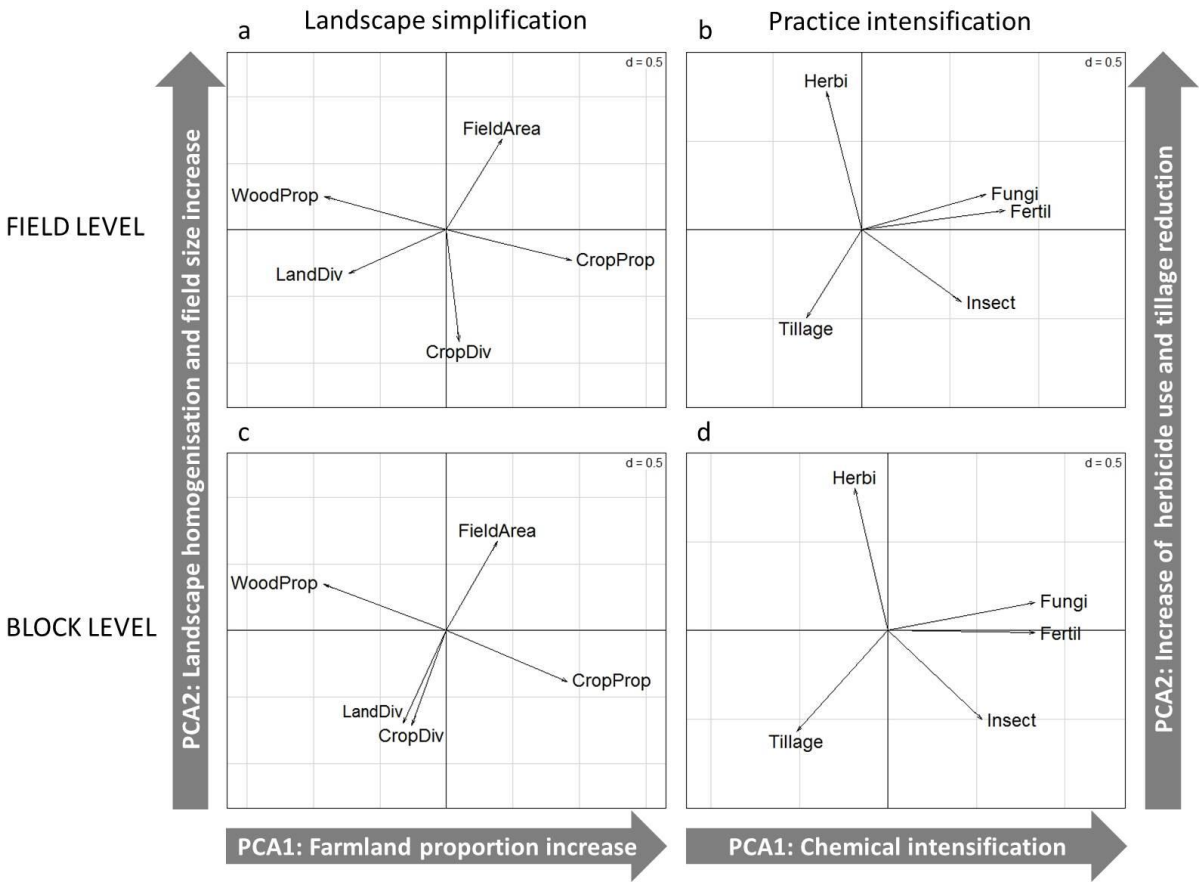
Landscape simplification
Practice intensification
a
b
c
d
d = 0.5
FieldArea
WoodProp
LandDiv
CropProp
CropDiv
Herbi
Fungi
Fertil
Insect
Tillage
FIELD LEVEL
BLOCK LEVEL
PCA2: Landscape homogenisation and field size increase
PCA2: Increase of herbicide use and tillage reduction
PCA1: Farmland proportion increase
PCA1: Chemical intensification

Figure 3

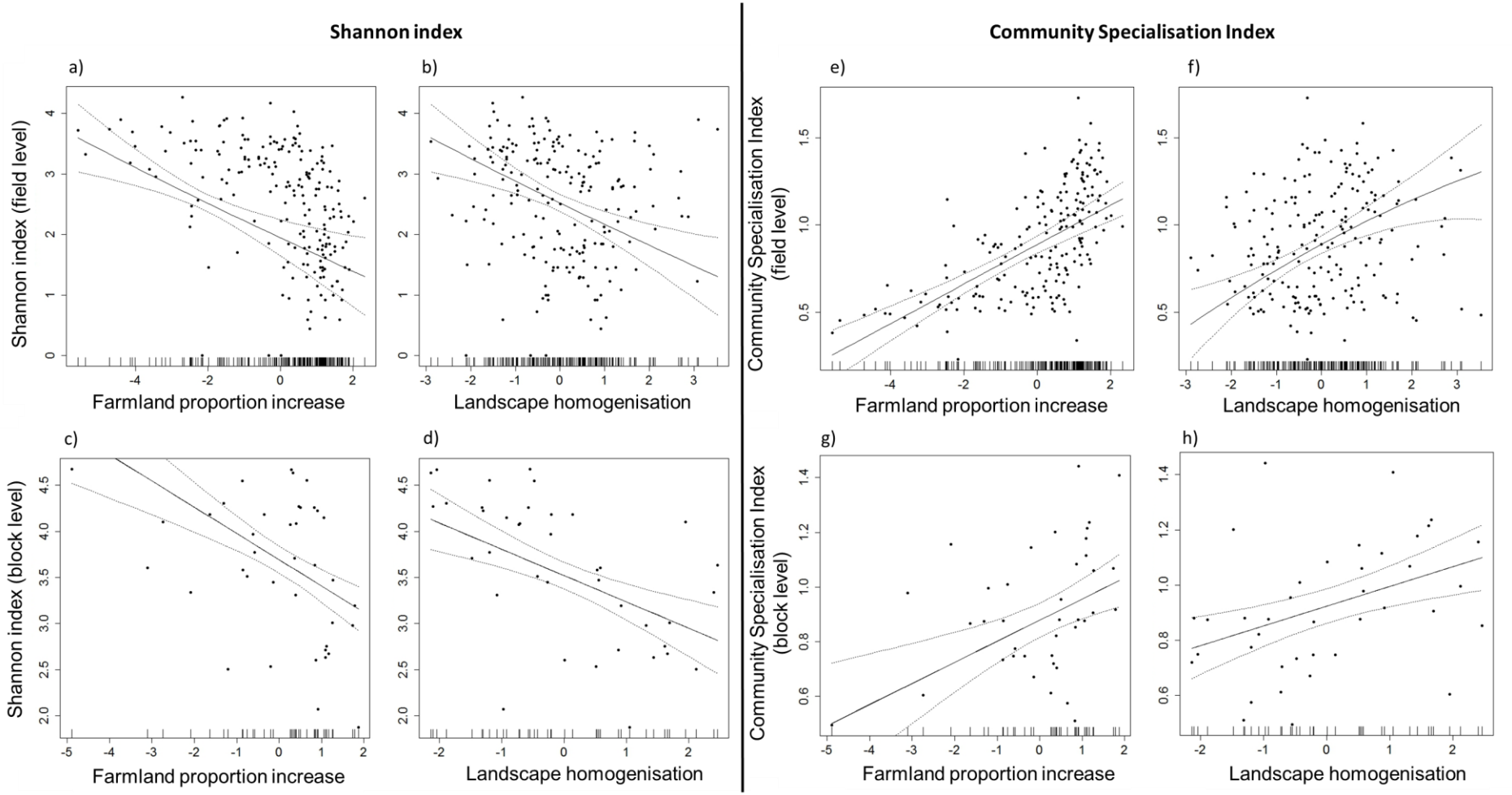
Shannon index
Community Specialisation Index
a)
b)
c)
d)
e)
f)
g)
h)
Shannon index (field level)
Shannon index (block level)
Community Specialisation Index (field level)
Community Specialisation Index (block level)
Farmland proportion increase
Landscape homogenisation

Figure 4

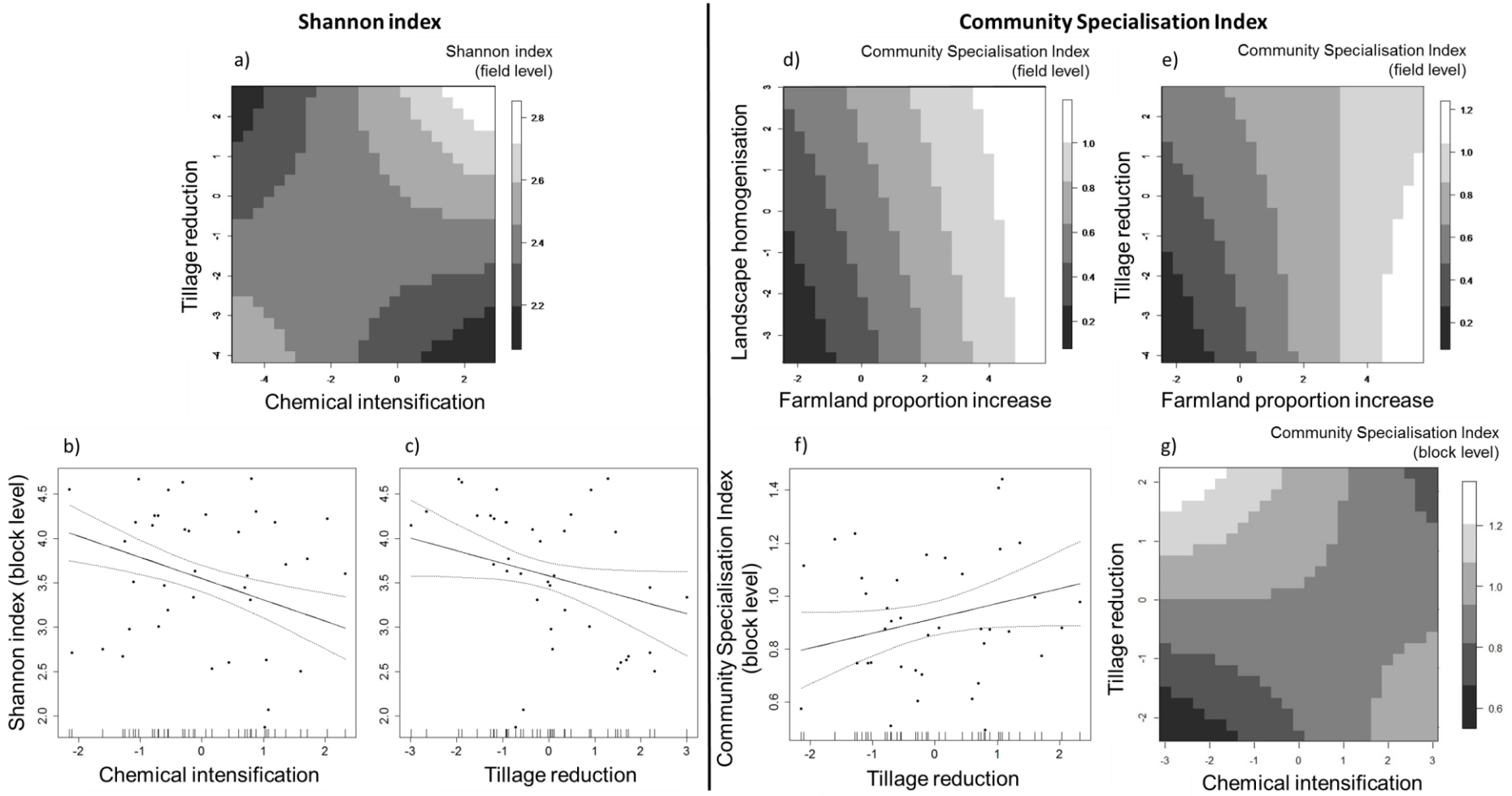
Shannon index
a)
Shannon index
(field level)
Tillage reduction
Chemical intensification
b)
Shannon index (block level)
Chemical intensification
c)
Tillage reduction
Community Specialisation Index
d)
Community Specialisation Index
(field level)
Landscape homogenisation
Farmland proportion increase
e)
Community Specialisation Index
(field level)
Tillage reduction
Farmland proportion increase
f)
Community Specialisation Index
(block level)
Tillage reduction
g)
Community Specialisation Index
(block level)
Tillage reduction
Chemical intensification

Figure 5

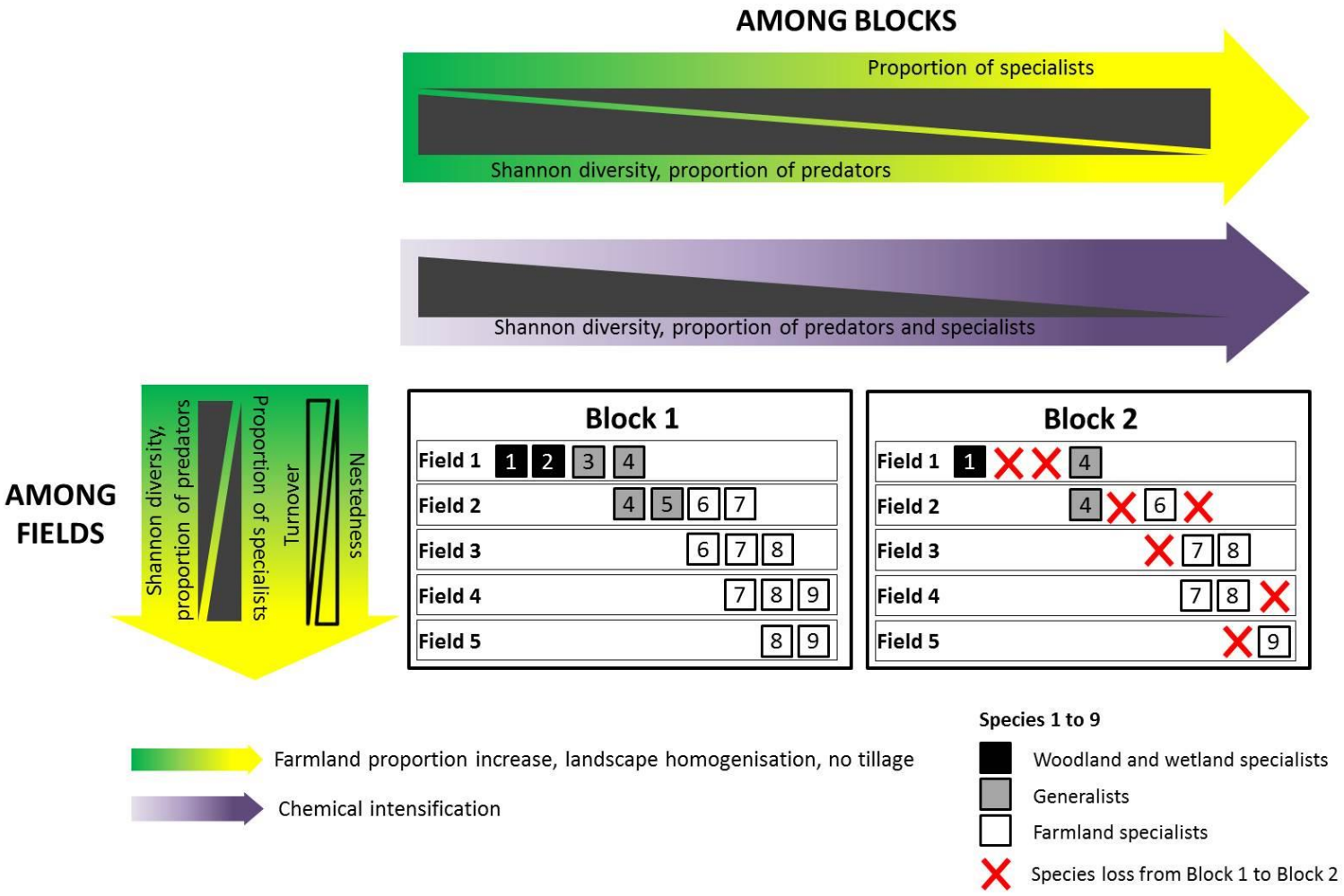
AMONG BLOCKS
Proportion of specialists
Shannon diversity, proportion of predators
Shannon diversity, proportion of predators and specialists
AMONG FIELDS
Shannon diversity, proportion of predators
Proportion of specialists
Turnover
Nestedness
Block 1
Field 1 1 2 3 4
Field 2 4 5 6 7
Field 3 6 7 8
Field 4 7 8 9
Field 5 8 9
Block 2
Field 1 1 4
Field 2 4 6
Field 3 7 8
Field 4 7 8
Field 5 9
Farmland proportion increase, landscape homogenisation, no tillage
Chemical intensification
Species 1 to 9
Woodland and wetland specialists
Generalists
Farmland specialists
Species loss from Block 1 to Block 2

Figure legends

Figure 1: Maps with a representation of the nested design used in the study in three French departments including 39 blocks of 4-5 fields in which birds were counted at two opposite points. Landscape and crop diversity were assessed around fields (300-m buffer areas centred on bird count points) and blocks (1500-m buffer areas centred on block centroids). Of the 199 fields studied, 26 were in Aisne, 46 in Charente-Maritime, and 127 in Yonne.

Figure 2: Plots representing the gradients of landscape simplification (a, c) and practice intensification (b, d) according to PCA analyses performed on (a, c) field area, crop and woodland cover proportions, and crop and land cover diversity; and on (b, d) the frequency of herbicide, fungicide, insecticide and fertiliser use, and tillage intensity. The first two axes (PCA1 and PCA2) were retained, together explaining a) 77%, b) 53%, c) 74%, and d) 63% of the total inertia of the data.

Figure 3: Plots of the key relationships between the gradients of landscape simplification (i.e. farmland proportion increase, landscape homogenisation), and the Shannon index (a-d), and the Community Specialisation Index (e-h), at field (1st line, a, b, e, f) and block (2nd line, c, d, g, h) levels resulting from linear mixed modelling analyses. In plots, solid black lines represent the model predictions; dashed black lines represent the 95% confidence intervals.

Figure 4: Plots of the key relationships between the gradients of agricultural practices (i.e. chemical intensification, tillage reduction), and the Shannon index (a-c), and the Community Specialisation Index (d-g), and of the interaction effects between landscape and practices (a, d, e, g), at field (1st line, a, d, e) and block (2nd line, b, c, f, g) levels resulting from linear mixed modelling analyses. In plots, solid black lines represent the model predictions; dashed black lines represent the 95% confidence intervals.

Figure 5: Schematic summary of the taxonomic and functional bird responses to gradients of agricultural intensification at field and block levels.

Tables

Table 1: Linear Mixed Modelling and Model Averaging analyses of the Shannon index, Community Specialisation Index (CSI) and Community Trophic Index (CTI) according to the gradients of agricultural intensification at the field level. The best random structure correcting for the nested design of fields within blocks (on intercept, as 1|Block, or on intercept and slope, Opening|Block) was chosen by comparing model AIC. Imp.: relative importance of the variables according to model-averaging outputs. The significant variables (Imp. >= 0.5) are represented in bold; R^2: percentage of variance explained by the final model.

		Field level								
		Shannon index			CSI			CTI		
	Random structure	1|Block			Opening|Block			1|Block		
		R^2 = 0.33			R^2 = 0.53			R^2 = 0.19		
	Model terms	Coef	SE	Imp.	Coef	SE	Imp.	Coef	SE	Imp.
	Intercept	2.523	0.073	-	0.888	0.026	-	1.502	0.01	-
Landscape simplification	Farmland proportion increase	**-0.282**	**0.043**	**1**	**0.11**	**0.013**	**1**	**-0.032**	**0.006**	**1**
	Homogenisation	**-0.102**	**0.053**	**0.76**	**0.033**	**0.016**	**0.86**	0.003	0.008	0.12
Practice intensification	Chemical intensification	-0.02	0.052	0.15	-0.006	0.015	0.13	-0.008	0.008	0.27
	Tillage reduction	0.025	0.06	0.15	-0.018	0.017	0.27	0.008	0.009	0.25
Interactions	Farmland prop. increase*Homogenisation	-0.021	0.029	0.2	**0.012**	**0.008**	**0.52**	0.002	0.005	0.12
	Farmland prop. increase*Chemical intensification	-0.016	0.032	0.16	0.004	0.009	0.13	**-0.007**	**0.005**	**0.5**
	Farmland prop. increase*Tillage reduction	-0.017	0.044	0.13	**0.021**	**0.012**	**0.67**	0.000	0.007	0.1
	Homogenisation*Chemical intensification	-0.042	0.038	0.29	0.01	0.01	0.28	-0.001	0.006	0.11
	Homogenisation*Tillage reduction	0.023	0.059	0.14	-0.016	0.016	0.28	0.010	0.009	0.34
	Chemical intensification*Tillage reduction	0.056	0.04	0.49	-0.01	0.011	0.22	0.003	0.007	0.14

Table 2: Linear Mixed Modelling and Model Averaging analyses of the Shannon index, Community Specialisation Index (CSI) and Community Trophic Index (CTI) according to the gradients of agricultural intensification at the block level. The best random structure correcting for the nested design of blocks within SARs (on intercept, as 1|SAR) was chosen by comparing model AIC. Imp.: relative importance of the variables according to model averaging outputs. The significant variables (Imp. >= 0.5) are represented in bold; R^2: percentage of variance explained by the final model.

		Block level								
		Shannon index			CSI			CTI		
	Random structure	1|SAR			1|SAR			1|SAR		
		R^2 = 0.64			R^2 = 0.44			R^2 = 0.20		
	Model terms	Coef	SE	Imp.	Coef	SE	Imp.	Coef	SE	Imp.
	Intercept	3.593	0.078	-	0.901	0.033	-	1.517	0.018	-
Landscape simplification	Farmland proportion increase	**-0.285**	**0.059**	**1**	**0.077**	**0.023**	**1**	-0.013	0.011	0.2
	Homogenisation	**-0.284**	**0.074**	**1**	**0.072**	**0.023**	**1**	-0.009	0.011	0.08
Practice intensification	Chemical intensification	**-0.154**	**0.065**	**0.92**	0.008	0.025	0.08	-0.012	0.01	0.2
	Tillage reduction	**-0.240**	**0.073**	**1**	**0.063**	**0.028**	**0.89**	0.008	0.013	0.08
Interactions	Farmland prop. increase*Homogenisation	-0.028	0.047	0.09	-0.001	0.019	0.07	**-0.020**	**0.009**	**0.84**
	Farmland prop. increase*Chemical intensification	-0.027	0.043	0.09	0.003	0.020	0.07	-0.003	0.008	0.07
	Farmland prop. increase*Tillage reduction	0.028	0.054	0.09	-0.014	0.018	0.1	-0.008	0.009	0.12
	Homogenisation*Chemical intensification	-0.019	0.04	0.08	0.025	0.015	0.48	**-0.014**	**0.008**	**0.58**
	Homogenisation*Tillage reduction	0.013	0.058	0.08	0.021	0.033	0.09	0.003	0.011	0.05
	Chemical intensification*Tillage reduction	0.049	0.051	0.13	**-0.047**	**0.021**	**0.9**	-0.001	0.010	0.05

Table 3: Multiple Regressions on distance Matrices analyses performed on the total beta diversity (JacTOT) based on Jaccard dissimilarities, and its two components, turnover (JacTU) and nestedness (JacNE) depending on the gradients of agricultural intensification and their interactions, the matrix of inter-site (field/block) spatial distances (Distance) and the neighbour matrix accounting for the nested design of sites, at block and SAR levels. The significant variables (P <= 0.05) are represented in bold; R^2: percentage of variance explained by the final model. Note that the R^2 values here are indicated for comparative purposes only among MRM results but are not directly comparable with R^2 values from the univariate models (LMM and LM), the two regression methods being different (Legendre and Fortin, 2010; Legendre and Legendre, 2012)

		Block (inter-field) level						SAR (inter-block) level					
		JacTOT		JacTU		JacNE		JacTOT		JacTU		JacNE	
		R^2 = 0.1		R^2 = 0.07		R^2 = 0.02		-		R^2 = 0.01		-	
	Model terms	Coef	P	Coef	P	Coef	P	Coef	P	Coef	P	Coef	P
	Intercept	0.699	1.000	0.550	1.000	0.149	0.057	0.663	0.674	0.548	0.728	0.115	0.572
Landscape simplification	Farmland proportion increase	**-0.031**	**0.001**	**-0.049**	**0.001**	**0.018**	**0.007**	0.013	0.299	0.003	0.827	0.010	0.281
	Homogenisation	**-0.011**	**0.014**	-0.008	0.483	-0.003	0.729	0.000	0.973	-0.007	0.608	0.008	0.518
Practice intensification	Chemical intensification	0.007	0.094	0.013	0.166	-0.006	0.394	0.005	0.699	-0.003	0.809	0.000	0.448
	Tillage disintensification	0.001	0.813	0.007	0.528	-0.006	0.492	0.007	0.618	-0.005	0.707	0.000	0.308
Interactions	Farmland prop. increase*Homogenisation	**0.005**	**0.002**	**0.006**	**0.050**	-0.001	0.698	-0.005	0.228	-0.001	0.870	-0.004	0.212
	Farmland prop. increase*Chemical intensification	0.000	0.841	-0.001	0.720	0.000	0.701	0.003	0.416	0.000	0.874	0.000	0.502
	Farmland prop. increase*Tillage reduction	0.002	0.067	**0.006**	**0.041**	-0.004	0.090	0.001	0.862	0.000	0.997	0.000	0.789
	Homogenisation*Chemical intensification	-0.001	0.364	-0.004	0.192	0.003	0.250	-0.008	0.091	-0.003	0.429	0.000	0.256
	Homogenisation*Tillage reduction	0.002	0.259	0.001	0.696	0.000	0.841	-0.008	0.084	-0.007	0.207	0.000	0.730
	Chemical intensification*Tillage reduction	-0.002	0.150	-0.004	0.294	0.002	0.543	0.003	0.390	0.004	0.393	0.000	0.871
Spatial components	Distance(fields/blocks)	**0.000**	**0.001**	**0.000**	**0.001**	**0.000**	**0.043**	0.000	0.177	**0.000**	**0.041**	0.000	0.537
	NeighbourMatrix(blocks/SAR)	**0.042**	**0.001**	**0.042**	**0.001**	0.000	0.976	-0.010	0.534	-0.020	0.157	0.010	0.416

Table 4: Linear Modelling analyses of species influences SpInf in patterns of total beta diversity (SpInf in JacTOT) and of its components of turnover (SpInf in JacTU) and nestedness (SpInf in JacNE) according to the four functional traits SSI, STI, Occurrence frequency and Status NF (Non-Farmland). In bold, significant variables; R^2: percentage of variance explained by the final model. Species influences for JacTOT and JacNE (-) were not testable since the MRM models for these diversities were not significant (see Table 3)

	Block (inter-field) level									SAR (inter-block) level								
	SpInf in JacTOT			SpInf in JacTU			SpInf in JacNE			SpInf in JacTOT			SpInf in JacTU			SpInf in JacNE		
	R^2 = 0.41			R^2 = 0.36			R^2 = 0.39			-			R^2 = 0.36			-		
Model terms	Coef	SE	P	Coef	SE	P	Coef	SE	P	Coef	SE	P	Coef	SE	P	Coef	SE	P
Intercept	0.379	0.095	**0.000**	0.293	0.114	**0.014**	0.188	0.136	0.175	-	-	-	0.082	0.115	0.483	-	-	-
SSI	-0.114	0.039	**0.006**	-0.069	0.049	0.170	0.023	0.061	0.704	-	-	-	0.042	0.055	0.452	-	-	-
STI	-0.010	0.037	0.789	0.010	0.040	0.800	-0.007	0.054	0.893	-	-	-	0.004	0.041	0.917	-	-	-
Occ. frequency (%)	0.003	0.002	0.152	0.005	0.002	**0.035**	0.010	0.002	**0.000**	-	-	-	0.004	0.001	**<0.001**	-	-	-
Status NF	-0.108	0.036	**0.005**	-0.150	0.047	**0.003**	-0.120	0.066	0.075	-	-	-	-0.001	0.044	0.974	-	-	-

Supplementary data

Appendix A. Supplementary materials and methods

Appendix B. Template of questionnaire to farmers about their agricultural practices

Appendix C. List of the 76 bird species used for the community analyses (Table C.1)

Appendix D. Full outputs of the model averaging analyses (Tables D.1 & D.2)

Appendix A. Supplementary materials and methods

Additional description of the study area

The Yonne department (Fig. 1c) is covered by more than 495,000 hectares of agricultural farmland (66% of the total area). The rest of the area corresponds mainly to forest and semi-natural habitats (30%). The Aisne department (Fig. 1b) is intensively cropped (65% of arable land). Like in Yonne, open cereal fields constitute a typical farmland landscape in Aisne. The Charente-Maritime department (Fig. 1d) is 77% cropped. This proportion includes intensive agricultural areas, but also heterogeneous arable landscapes with pastures and small fields interspaced by bushes and woody areas. Forest and semi-natural habitats represent only 16% of the area of the department.

Additional information on statistical methods

- Handling of multi-collinearity in all models

The multi-collinearity of landscape and practice gradients was tested by diagnosing the Variance Inflation Factors (VIF, R package {AED}; Zuur, 2010). This diagnosis conditioned the ability to disentangle their respective effects on biotic responses and enabled their main and interaction effects to be tested.

Similarly, in the analysis of species-specific contributions, the multi-collinearity of the four trait variables (Species Specialisation Index, Species Trophic Index, Occurrence frequency and Farmland Status) included in the linear regression was checked previously by the VIF diagnosis.

For both analyses, the multi-collinearity of the variables involved in the models was reasonable since their variance inflation factor was below 2 (Graham, 2003).

- Handling of spatial structure in all models

For the analyses of alpha/gamma responses to the gradients of agricultural intensification, using mixed modelling, we verified that the spatial dependence of the response variable was appropriately handled by the random structure of the mixed models. To do so, we systematically proceeded to the spatial diagnosis of model residuals through the analysis of their semi-variograms (Zuur et al., 2009).

For the *explanation* of beta diversity *variations* (to be distinguished from *analysis of beta diversity*, see the scientific discussion about distinction of “Analysing or explaining beta diversity?” initiated by (Legendre et al., 2005) according to the gradients of agricultural intensification, Multiple Regressions on distance Matrices were used, as recommended by Tuomisto & Ruokalainen (2006). The nested structure of the design was reflected in the

MRM models. To do so, contingency tables were built that encoded by 0 or 1 the inclusion of sites in higher-level entities. For example, in the table for the analysis at the block level (inter-field), lines were fields and columns were block IDs. At each line, there was only one value “1” indicating that the field of this line was nested in the corresponding block, and not in the others (value “0”) (principle of dummy coding). The same principle was applied to the SAR level (inter-block). These tables enabled neighbour matrices to be calculated (e.g. Dray et al., 2006) reflecting inter-site dependence due to the nested structure of the design, which were included in the MRM models.

To assess the significance of association between the response matrix and the other distance matrices, the randomisation procedure consists in randomly permuting the rows and associated columns of the response matrix (leading to a kind of null model) and then determining whether regression coefficients of the relationship between the permuted response matrix and the other distance matrices are absolutely higher than expected by chance. This procedure is repeated 999 times.

- Details on the analysis of species trait influence

In line with Davey et al. (2013), to determine which and how species traits effectively influenced beta diversity components, only species whose influence was greater than zero were included (at the block level: for *JacTU*, n=46, and for *JacNE*, n=43, at the SAR level: for *JacTU*, n=38 species). To handle such proportion data properly, the regression was applied on the arcsine square root transformed variable *asin[sqrt(SpInf)]*.

Appendix B. Template of questionnaire to farmers about their agricultural practices

Last name _____ First name _____

Code number of the studied field (see map):_____

A) Crop and environmental characteristics of the studied field in 2010

1- What is the crop type growing? _____

2- What is the standard crop rotation? _____

3- What are the crop types growing on fields adjacent to the studied field?

	Crops on adjacent fields (in 2010)		**Crops on adjacent fields (in 2010)**
N°1		N°6	
N°2		N°7	
N°3		N°8	
N°4		N°9	
N°5		N°10	

5- How was the soil of the studied field prepared in 2010? (Full conventional tillage, conservation tillage like non-inversion tillage, or no tillage)? _____

B) Pesticide use practices on the studied field in 2010

Has studied field been treated with pesticides in 2010? ☐ yes ☐ no

Please, give as much details as possible about treatments used in 2010 (pesticide commercial name, field area covered, doses and application dates).

	Commercial name of the plant protection product used in 2010	**Dose in l/ha or kg/ha**	**Dates of application** **1 line per application**
Fertiliser (number of NPK units, chemical or organic)			
Insecticides			

(spray)			
Fungicides (spray)			
Herbicides (spray)			
Seed treatments, Plant growth regulator			

2- Has the same field been treated with pesticides in **2009**? ☐ yes ☐ no

3- What was the crop growing in **2009**? _____

Has studied field been treated with pesticides in **2009**? ☐ yes ☐ no

Please, give as much details as possible about treatments used in **2009** (pesticide commercial name, field area covered, doses and application dates).

	Commercial name of the plant protection product used in 2009	**Dose in l/ha or kg/ha**	**Dates of application** **1 line per application**
Fertiliser (number of NPK units, chemical or organic)			
Insecticides (spray)			
Fungicides (spray)			

Herbicides (spray)			
Seed treatments, Plant growth regulator			

177

178

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Appendix C. List of the 76 bird species used for the community analyses

Table C.1: List of the 76 bird species used for the community analyses. Species were sorted according to their status (F: farmland *vs*. NF: non-farmland, from Jiguet et al., 2012, and based on the Farmland Bird Index in France; Jiguet et al., 2010) to which we added three species typical of French lowland agricultural areas: the Barn Swallow, the Montagu's Harrier, and the Stone Curlew. Species Specialisation Index and Species Trophic Index values were computed from Julliard et al. (2006) and Princé et al. (2013), respectively. Species occurrence frequency was calculated over the 199 studied fields. Among all the birds observed, four species were excluded from the analysis: Grey Partridge (*Perdix perdix*), Red-legged partridge (*Alectoris rufa*), Common Pheasant (*Phasianus colchicus*) and Mallard (*Anas platyrhyncos*), because their abundance can be locally biased by annual releases for hunting purposes.

English and Latin species name	Species status	Species Trophic Index (STI)	Species Specialisation Index (SSI)	Occurrence frequency (%)
Barn Swallow (*Hirundo rustica*)	F	2.00	0.72	16
Cirl Bunting (*Emberiza cirlus*)	F	1.30	0.59	7
Common Buzzard (*Buteo buteo*)	F	2.90	0.49	6
Common Kestrel (*Falco tinnunculus*)	F	2.85	0.68	5
Common Quail (*Coturnix coturnix*)	F	1.22	1.52	21
Common Stonechat (*Saxicola rubicola*)	F	2.00	0.78	5
Corn Bunting (*Emberiza calandra*)	F	1.28	1.46	35
Common Whitethroat (*Sylvia communis*)	F	1.60	0.65	26
Hoopoe (*Upupa epops*)	F	2.00	0.61	1
Linnet (*Carduelis cannabina*)	F	1.05	0.70	15
Meadow Pipit (*Anthus pratensis*)	F	1.75	1.37	2
Montagu's Harrier (*Circus pygargus*)	F	2.60	1.69	2
Northern Lapwing (*Vanellus vanellus*)	F	1.90	2.23	1
Northern Wheatear (*Oenanthe oenanthe*)	F	1.95	1.70	2
Red-backed Shrike (*Lanius collurio*)	F	2.15	1.14	5
Rook (*Corvus frugilegus*)	F	1.63	0.85	1

Skylark (*Alauda arvensis*)	F	1.25	1.16	82
Stone Curlew (*Burhinus oedicnemus*)	F	1.95	1.90	1
Wood Lark (*Lullula arborea*)	F	1.50	0.90	4
Yellow Wagtail (*Motacilla flava*)	F	2.00	2.09	46
Yellowhammer (*Emberiza citrinella*)	F	1.30	0.71	16
Black Kite (*Milvus migrans*)	NF	2.83	0.75	2
Black Redstart (*Phoenicurus ochruros*)	NF	1.85	1.12	8
Black Woodpecker (*Dryocopus martius*)	NF	2.00	1.24	1
Black-billed Magpie (*Pica pica*)	NF	1.51	0.70	6
Blackbird (*Turdus merula*)	NF	1.60	0.23	44
Blackcap (*Sylvia atricapilla*)	NF	1.60	0.32	47
Blue Tit (*Cyanistes caeruleus*)	NF	1.80	0.35	22
Bonelli's Warbler (*Phylloscopus bonelli*)	NF	2.00	0.86	4
Carrion Crow (*Corvus corone*)	NF	1.51	0.28	18
Cetti's Warbler (*Cettia cetti*)	NF	2.00	1.36	2
Chaffinch (*Fringilla coelebs*)	NF	1.10	0.27	44
Collared Dove (*Streptopelia decaocto*)	NF	1.00	0.99	12
Common Chiffchaff (*Phylloscopus collybita*)	NF	1.95	0.46	28
Common Cuckoo (*Cuculus canorus*)	NF	2.00	0.43	3
Common Redstart (*Phoenicurus phoenicurus*)	NF	1.93	0.97	4
Common Starling (*Sturnus vulgaris*)	NF	1.50	0.57	15

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193 **Table C.1.** Continued

English and Latin species name	Species status	Species trophic index (SSI)	Species specialisation index (SSI)	Occurrence (%)
Dunnock (*Prunella modularis*)	NF	1.50	0.50	8
Eurasian Bullfinch (*Pyrrhula pyrrhula*)	NF	1.10	1.05	1
Firecrest (*Regulus ignicapillus*)	NF	2.00	1.08	3
Garden Warbler (*Sylvia borin*)	NF	1.60	0.69	13
Golden Oriole (*Oriolus oriolus*)	NF	1.95	0.47	6
Goldfinch (*Carduelis carduelis*)	NF	1.05	0.70	10
Grasshopper Warbler (*Locustella naevia*)	NF	2.00	1.24	1
Great Spotted Woodpecker (*Dendrocopos major*)	NF	1.70	0.64	4
Great Tit (*Parus major*)	NF	1.85	0.29	30
Green Woodpecker (*Picus viridis*)	NF	2.00	0.38	4
Greenfinch (*Carduelis chloris*)	NF	1.05	0.66	13
Grey Heron (*Ardea cinerea*)	NF	2.85	1.14	1
Hawfinch (*Coccothrautes coccothrautes*)	NF	1.05	0.98	1
Hen Harrier (*Circus cyaneus*)	NF	3.00	1.25	1
Hobby (*Falco subbuteo*)	NF	2.25	1.50	3
House Martin (*Delichon urbicum*)	NF	2.00	1.27	3
House Sparrow (*Passer domesticus*)	NF	1.20	1.26	18
Jay (*Garrulus glandarius*)	NF	1.72	0.44	8
Lesser Spotted Woodpecker (*Dendrocopos minor*)	NF	2.00	0.91	1
Long-tailed Tit (*Aegithalos caudatus*)	NF	1.95	0.62	3
Marsh Tit (*Poecile palustris*)	NF	1.70	0.99	1
Melodious Warbler (*Hippolais polyglotta*)	NF	1.95	0.70	19
Middle Spotted Woodpecker (*Dendrocopos medius*)	NF	1.70	1.92	1
Mistle Thrush (*Turdus viscivorus*)	NF	1.55	0.52	3

194 **Table C.1.** Continued

English and Latin species name	Species status	Species trophic index (SSI)	Species specialisation index (SSI)	Occurrence (%)
Common Nightingale (*Luscinia megarhynchos*)	NF	2.00	0.47	19
Serin (*Serinus serinus*)	NF	1.00	0.78	5
Short-toed Treecreeper (*Certhia brachydactyla*)	NF	2.00	0.62	5
Song Thrush (*Turdus philomelos*)	NF	1.57	0.40	12
Sparrowhawk (*Accipiter nisus*)	NF	3.00	0.79	1
Stock Pigeon (*Columba oenas*)	NF	1.01	1.29	1
Tree Pipit (*Anthus trivialis*)	NF	1.95	0.91	16
Turtle Dove (*Streptopelia turtur*)	NF	1.00	0.40	14
White Wagtail (*Motacilla alba*)	NF	2.00	0.69	12
Willow warbler (*Phylloscopus trochilus*)	NF	1.95	1.12	6
Eurasian Nuthatch (*Sitta europaea*)	NF	1.63	0.92	4
Wood Pigeon (*Columba palumbus*)	NF	1.01	0.30	31
Woodchat Shrike (*Lanius senator*)	NF	2.05	1.24	1
Wren (*Troglodytes troglodytes*)	NF	2.00	0.37	15

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Appendix D. Full outputs of the model averaging analyses after model selection

Table D.1: Subset of the best models resulting from the model averaging procedure, fitted on Shannon, CSI and CTI indices according to the four variables of agricultural intensification, and interaction terms at the field level. Variables are coded from 1 to 10, for the four simple effects (7-10) plus the six interaction effects (1-6), df: degrees of freedom of the model, logLik: log-likelihood, AICc: corrected Akaïke Information Criterion, delta: AICc difference between the model and the best model (delta-AICc<4), weight: Akaïke weight of the model (used for calculating relative importance of model parameters at the end of the model averaging procedure). Models are ranked with their AICc.

Shannon						CSI						CTI					
Variables	**df**	**logLik**	**AICc**	**delta**	**weight**	**Variables**	**df**	**logLik**	**AICc**	**delta**	**weight**	**Variables**	**df**	**logLik**	**AICc**	**delta**	**weight**
6/7/8	6	-238.0856	488.6088	0	0.0554	1/3/7/8	9	20.9401	-22.9279	0	0.0379	7	4	120.9222	-233.6382	0	0.0556
7/8	5	-239.2247	488.7603	0.1516	0.0514	3/7/8	8	19.6855	-22.6131	0.3148	0.0324	2/7	5	121.9163	-233.5217	0.1165	0.0525
4/7/8	6	-238.484	489.4055	0.7967	0.0372	7/8	7	18.5373	-22.4882	0.4396	0.0304	2/5/7	6	122.6763	-232.9151	0.7231	0.0388
4/6/7/8	7	-237.637	489.8605	1.2517	0.0297	3/7/8/10	9	20.5031	-22.0539	0.874	0.0245	5/7	5	121.5882	-232.8656	0.7726	0.0378
7	4	-240.8686	489.9434	1.3346	0.0285	1/3/5/7/8	10	21.6115	-22.0528	0.875	0.0245	2/7/9	6	122.4586	-232.4797	1.1585	0.0312
1/7/8	6	-238.9535	490.3444	1.7356	0.0233	1/3/7/8/10	10	21.525	-21.8797	1.0481	0.0224	7/9	5	121.3007	-232.2905	1.3476	0.0284
1/6/7/8	7	-237.8823	490.351	1.7422	0.0232	1/3/4/7/8	10	21.4436	-21.717	1.2108	0.0207	7/10	5	121.2657	-232.2206	1.4176	0.0274
5/6/7/8	7	-237.8831	490.3526	1.7438	0.0232	1/7/8	8	19.2133	-21.6688	1.2591	0.0202	2/7/10	6	122.322	-232.2064	1.4317	0.0272
6/7	5	-240.0542	490.4193	1.8106	0.0224	3/4/7/8	9	20.2809	-21.6095	1.3184	0.0196	1/7	5	121.0116	-231.7124	1.9258	0.0212
2/7/8	6	-239.0313	490.5001	1.8913	0.0215	4/7/8	8	19.1664	-21.5749	1.3529	0.0193	7/8	5	120.9766	-231.6423	1.9958	0.0205
4/7	5	-240.1002	490.5114	1.9026	0.0214	1/3/5/6/7/8	11	22.4136	-21.4154	1.5125	0.0178	2/5/7/9	7	123.1065	-231.6265	2.0116	0.0203
6/7/8/10	7	-237.9635	490.5134	1.9046	0.0214	7/8/10	8	19.0484	-21.3389	1.5889	0.0171	4/7	5	120.9441	-231.5773	2.0608	0.0199
6/7/8/9	7	-237.9944	490.5752	1.9665	0.0207	1/3/6/7/8	10	21.1843	-21.1983	1.7295	0.016	6/7	5	120.9357	-231.5606	2.0776	0.0197
3/6/7/8	7	-237.9955	490.5773	1.9686	0.0207	3/6/7/8	9	20.0146	-21.0769	1.851	0.015	3/7	5	120.9233	-231.5357	2.1025	0.0194
2/6/7/8	7	-238.008	490.6025	1.9937	0.0205	1/3/4/5/7/8	11	22.2402	-21.0686	1.8592	0.015	1/2/7	6	121.985	-231.5325	2.1057	0.0194
3/7/8	6	-239.135	490.7076	2.0988	0.0194	1/3/7	8	18.9028	-21.0477	1.8802	0.0148	2/5/7/10	7	123.014	-231.4417	2.1965	0.0185
7/8/10	6	-239.1423	490.7222	2.1134	0.0193	3/5/7/8	9	19.948	-20.9436	1.9843	0.014	2/7/8	6	121.9363	-231.435	2.2031	0.0185

Variable codes: 1=Farm. prop. increase*Land. homogenisation, **2**=Farm. prop. increase*Chemic. intensification, **3**=Farm. prop. increase*Tillage reduction, **4**=Land. homogenisation*Chemic. intensification, **5**=Land. homogenisation*Tillage reduction, **6**=Chemic. intensification*Tillage reduction, **7**=Farm. prop. increase, **8**=Land. homogenisation, **9**=Chemic. intensification, **10**=Tillage reduction

Table D.1. Continued

Shannon						CSI						CTI					
Variables	**df**	**logLik**	**AICc**	**delta**	**weight**	**Variables**	**df**	**logLik**	**AICc**	**delta**	**weight**	**Variables**	**df**	**logLik**	**AICc**	**delta**	**weight**

7/8/9	6	-239.2062	490.85	2.2412	0.0181	1/7	7	17.7336	-20.8809	2.047	0.0136	2/3/7	6	121.9361	-231.4346	2.2036	0.0185
5/7/8	6	-239.217	490.8714	2.2626	0.0179	6/7/8	8	18.8139	-20.8699	2.0579	0.0135	2/4/7	6	121.9199	-231.4023	2.2358	0.0182
1/4/7/8	7	-238.2527	491.0918	2.4831	0.016	1/2/3/7/8	10	21.0173	-20.8643	2.0635	0.0135	2/6/7	6	121.9168	-231.3962	2.242	0.0181
2/4/7/8	7	-238.3404	491.2673	2.6585	0.0147	1/3/5/7/8/10	11	22.1292	-20.8467	2.0812	0.0134	5/6/7	6	121.8938	-231.35	2.2882	0.0177
1/7	5	-240.5301	491.3711	2.7624	0.0139	1/3/7/8/9	10	21.0054	-20.8406	2.0872	0.0133	5/7/9	6	121.8769	-231.3164	2.3218	0.0174
3/4/7/8	7	-238.4199	491.4263	2.8175	0.0136	3/4/7/8/10	10	20.9592	-20.7482	2.1797	0.0127	5/7/10	6	121.8722	-231.3068	2.3314	0.0173
4/7/8/10	7	-238.4436	491.4736	2.8648	0.0132	7	6	16.5886	-20.7398	2.1881	0.0127	2/5/6/7	7	122.8529	-231.1194	2.5187	0.0158
4/7/8/9	7	-238.4574	491.5012	2.8924	0.0131	2/7/8	8	18.716	-20.6742	2.2537	0.0123	2/7/9/10	7	122.8486	-231.1108	2.5273	0.0157
4/6/7	6	-239.5322	491.5019	2.8932	0.0131	1/4/7/8	9	19.7787	-20.6049	2.3229	0.0119	4/5/7	6	121.6492	-230.8609	2.7773	0.0139
4/5/7/8	7	-238.484	491.5543	2.9455	0.0127	3/7/8/9	9	19.7707	-20.5891	2.3388	0.0118	5/7/8	6	121.6462	-230.8549	2.7833	0.0138
4/5/6/7/8	8	-237.4204	491.5988	2.99	0.0124	2/3/7/8	9	19.7626	-20.5729	2.3549	0.0117	7/9/10	6	121.6339	-230.8303	2.8079	0.0137
1/4/6/7/8	8	-237.4539	491.6657	3.057	0.012	3/6/7/8/10	10	20.8619	-20.5537	2.3742	0.0116	2/4/5/7	7	122.7022	-230.818	2.8201	0.0136
2/7	5	-240.7279	491.7666	3.1579	0.0114	5/7/8	8	18.6553	-20.5527	2.3752	0.0116	2/5/7/8	7	122.6976	-230.8089	2.8293	0.0135
4/6/7/8/9	8	-237.5458	491.8495	3.2407	0.011	1/3/4/7/8/10	11	21.9253	-20.4388	2.4891	0.0109	3/5/7	6	121.6215	-230.8055	2.8327	0.0135
7/9	5	-240.7714	491.8536	3.2449	0.0109	1/3/5/7	9	19.6788	-20.4051	2.5227	0.0107	1/5/7	6	121.6183	-230.7992	2.839	0.0135
7/10	5	-240.7785	491.8679	3.2591	0.0109	7/8/9	8	18.5578	-20.3577	2.5702	0.0105	1/2/5/7	7	122.6914	-230.7964	2.8418	0.0134
4/6/7/8/10	8	-237.5608	491.8794	3.2706	0.0108	3/5/7/8/10	10	20.7452	-20.3202	2.6076	0.0103	2/3/5/7	7	122.6763	-230.7663	2.8719	0.0132
3/4/6/7/8	8	-237.5671	491.8921	3.2833	0.0107	1/3/5/6/7/8/10	12	22.9542	-20.2311	2.6968	0.0098	2/7/8/9	7	122.5462	-230.506	3.1322	0.0116
2/4/6/7/8	8	-237.5755	491.9089	3.3001	0.0106	3/5/6/7/8	10	20.6851	-20.1999	2.7279	0.0097	1/2/7/9	7	122.5378	-230.4893	3.1489	0.0115
1/5/6/7/8	8	-237.6051	491.9682	3.3594	0.0103	1/3/6/7/8/10	11	21.8015	-20.1912	2.7367	0.0096	7/8/9	6	121.4437	-230.4498	3.1884	0.0113
1/6/7	6	-239.7759	491.9893	3.3805	0.0102	4/7/8/10	9	19.5663	-20.1803	2.7475	0.0096	2/3/7/9	7	122.4854	-230.3845	3.2537	0.0109
5/7	5	-240.8613	492.0335	3.4247	0.01	1/7/8/10	9	19.5516	-20.1509	2.7769	0.0095	1/7/10	6	121.4005	-230.3635	3.2747	0.0108
3/7	5	-240.8622	492.0353	3.4266	0.01	3/7/8/9/10	10	20.6552	-20.1402	2.7876	0.0094	1/7/9	6	121.3986	-230.3598	3.2784	0.0108
1/4/7	6	-239.8122	492.0619	3.4531	0.0099	3/4/5/7/8	10	20.6411	-20.1119	2.816	0.0093	2/6/7/9	7	122.4622	-230.338	3.3002	0.0107
6/7/9	6	-239.8256	492.0887	3.48	0.0097	1/3/5/7/8/9	11	21.7575	-20.1032	2.8247	0.0092	2/4/7/9	7	122.4621	-230.3379	3.3003	0.0107
1/2/7/8	7	-238.7538	492.094	3.4852	0.0097	2/3/7/8/10	10	20.6116	-20.0531	2.8748	0.009	1/2/7/10	7	122.4321	-230.2778	3.3604	0.0104
1/3/7/8	7	-238.7759	492.1383	3.5295	0.0095	1/5/7/8	9	19.4823	-20.0122	2.9157	0.0088	6/7/9	6	121.338	-230.2386	3.3996	0.0102
1/3/6/7/8	8	-237.7164	492.1908	3.582	0.0092	1/3/4/5/6/7/8	12	22.8425	-20.0076	2.9202	0.0088	4/7/9	6	121.3263	-230.2151	3.4231	0.01
3/5/6/7/8	8	-237.73	492.2178	3.609	0.0091	1/2/3/5/7/8	11	21.6992	-19.9866	2.9413	0.0087	7/8/10	6	121.3118	-230.186	3.4522	0.0099

Variable codes: 1=Farm. prop. increase*Land. homogenisation, **2**=Farm. prop. increase*Chemic. intensification, **3**=Farm. prop. increase*Tillage reduction, **4**=Land. homogenisation*Chemic. intensification, **5**=Land. homogenisation*Tillage reduction, **6**=Chemic. intensification*Tillage reduction, **7**=Farm. prop. increase, **8**=Land. homogenisation, **9**=Chemic. intensification, **10**=Tillage reduction

Table D.1. Continued

Shannon						CSI						CTI					

Variables	df	logLik	AICc	delta	weight
5/6/7	6	-239.9254	492.2883	3.6796	0.0088
6/7/10	6	-239.9292	492.2959	3.6871	0.0088
1/6/7/8/9	8	-237.7766	492.3111	3.7023	0.0087
5/6/7/8/10	8	-237.7847	492.3274	3.7186	0.0086
1/6/7/8/10	8	-237.7943	492.3466	3.7378	0.0086
5/6/7/8/9	8	-237.7962	492.3503	3.7415	0.0085
1/2/6/7/8	8	-237.7986	492.3551	3.7463	0.0085
2/5/6/7/8	8	-237.8118	492.3814	3.7727	0.0084
1/7/8/10	7	-238.9015	492.3893	3.7806	0.0084
4/7/9	6	-239.9818	492.4011	3.7923	0.0083
2/7/8/10	7	-238.9252	492.4368	3.8281	0.0082
2/4/7	6	-240.0002	492.4379	3.8292	0.0082
1/7/8/9	7	-238.9259	492.4383	3.8295	0.0082
2/6/7	6	-240.0035	492.4445	3.8357	0.0081
1/5/7/8	7	-238.9534	492.4933	3.8845	0.008
2/6/7/8/10	8	-237.8708	492.4994	3.8906	0.0079
3/6/7/8/10	8	-237.8737	492.5052	3.8965	0.0079
2/3/7/8	7	-238.9734	492.5332	3.9244	0.0078
6/7/8/9/10	8	-237.8886	492.5352	3.9264	0.0078
3/6/7	6	-240.0495	492.5365	3.9277	0.0078
4/7/10	6	-240.0576	492.5526	3.9439	0.0077
2/6/7/8/9	8	-237.9073	492.5724	3.9637	0.0076
2/7/8/9	7	-239.0037	492.5937	3.985	0.0076
3/6/7/8/9	8	-237.9212	492.6003	3.9915	0.0075

Variables	df	logLik	AICc	delta	weight
1/6/7/8	9	19.429	-19.9056	3.0223	0.0084
1/2/7/8	9	19.419	-19.8856	3.0423	0.0083
1/3/7/8/9/10	11	21.6438	-19.8758	3.0521	0.0082
1/2/3/7/8/10	11	21.6275	-19.8433	3.0845	0.0081
3/4/6/7/8	10	20.4688	-19.7673	3.1605	0.0078
4/5/7/8	9	19.3545	-19.7567	3.1711	0.0078
1/3/4/6/7/8	11	21.5788	-19.7459	3.182	0.0077
6/7/8/10	9	19.3396	-19.7268	3.2011	0.0076
1/3/4/7	9	19.3186	-19.6849	3.243	0.0075
2/4/7/8	9	19.3147	-19.677	3.2508	0.0075
4/7	7	17.1316	-19.6767	3.2511	0.0075
4/6/7/8	9	19.3121	-19.6718	3.256	0.0074
1/4/7	8	18.2085	-19.659	3.2688	0.0074
3/7	7	17.1192	-19.6521	3.2757	0.0074
1/3/7/10	9	19.2905	-19.6287	3.2992	0.0073
1/3/4/5/7/8/10	12	22.644	-19.6107	3.3172	0.0072
2/7/8/10	9	19.2799	-19.6074	3.3204	0.0072
3/5/6/7/8/10	11	21.5092	-19.6067	3.3212	0.0072
1/3/4/7/8/9	11	21.5056	-19.5995	3.3284	0.0072
1/2/3/4/7/8	11	21.501	-19.5903	3.3376	0.0071
3/4/7/8/9	10	20.3599	-19.5496	3.3782	0.007
2/3/4/7/8	10	20.3383	-19.5064	3.4214	0.0068
1/7/8/9	9	19.2217	-19.4909	3.4369	0.0068
7/10	7	17.0358	-19.4851	3.4427	0.0068
1/5/7	8	18.1124	-19.467	3.4609	0.0067
4/7/8/9	9	19.1831	-19.4139	3.514	0.0065
5/6/7/8	9	19.1791	-19.4057	3.5221	0.0065
5/7/8/10	9	19.1433	-19.3342	3.5936	0.0063
1/3/5/6/7/8/9	12	22.4792	-19.281	3.6468	0.0061

Variables	df	logLik	AICc	delta	weight
3/7/9	6	121.3015	-230.1656	3.4726	0.0098
6/7/10	6	121.288	-230.1386	3.4996	0.0097
2/5/7/9/10	8	123.438	-230.1182	3.52	0.0096
4/7/10	6	121.273	-230.1085	3.5297	0.0095
2/3/7/10	7	122.3465	-230.1066	3.5316	0.0095
3/7/10	6	121.2663	-230.0951	3.543	0.0095
2/7/8/10	7	122.3361	-230.0858	3.5524	0.0094
2/4/7/10	7	122.3221	-230.0578	3.5804	0.0093
2/6/7/10	7	122.3221	-230.0577	3.5804	0.0093
2/5/6/7/9	8	123.3347	-229.9114	3.7268	0.0086
5/6/7/9	7	122.2438	-229.9012	3.737	0.0086
5/6/7/10	7	122.1942	-229.802	3.8362	0.0082
5/7/9/10	7	122.158	-229.7296	3.9086	0.0079
1/7/8	6	121.055	-229.6726	3.9656	0.0077
2/5/6/7/10	8	123.2022	-229.6465	3.9916	0.0076

Variable codes: 1=Farm. prop. increase*Land. homogenisation, **2**=Farm. prop. increase*Chemic. intensification, **3**=Farm. prop. increase*Tillage reduction, **4**=Land. homogenisation*Chemic. intensification, **5**=Land. homogenisation*Tillage reduction, **6**=Chemic. intensification*Tillage reduction, **7**=Farm. prop. increase, **8**=Land. homogenisation, **9**=Chemic. intensification, **10**=Tillage reduction

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206 **Table D.1.** Continued

CSI					
Variables	**df**	**logLik**	**AICc**	**delta**	**weight**
1/4/5/7/8	10	20.1358	-19.1015	3.8264	0.0056
1/3/4/5/7/8/9	12	22.3874	-19.0975	3.8304	0.0056
1/2/7	8	17.9265	-19.095	3.8328	0.0056
1/2/3/6/7/8	11	21.2307	-19.0497	3.8782	0.0054
1/2/3/7	9	18.9941	-19.0358	3.892	0.0054
1/3/6/7/8/9	11	21.2112	-19.0107	3.9172	0.0053
1/3/5/7/8/9/10	12	22.3432	-19.009	3.9188	0.0053
3/5/7/8/9	10	20.0861	-19.002	3.9259	0.0053
1/3/6/7	9	18.9748	-18.9971	3.9307	0.0053
3/4/6/7/8/10	11	21.1855	-18.9592	3.9686	0.0052
2/3/6/7/8	10	20.057	-18.9438	3.984	0.0052
3/4/5/6/7/8	11	21.1767	-18.9417	3.9862	0.0052
1/2/3/4/5/7/8	12	22.3058	-18.9342	3.9936	0.0051
3/6/7/8/9	10	20.0499	-18.9296	3.9983	0.0051

Variable codes: 1=Farm. prop. increase*Land. homogenisation, **2**=Farm. prop. increase*Chemic. intensification, **3**=Farm. prop. increase*Tillage reduction, **4**=Land. homogenisation*Chemic. intensification, **5**=Land. homogenisation*Tillage reduction, **6**=Chemic. intensification*Tillage reduction, **7**=Farm. prop. increase, **8**=Land. homogenisation, **9**=Chemic. intensification, **10**=Tillage reduction

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Table D.2: Subset of the best models resulting from the model averaging procedure, fitted on Shannon, CSI and CTI indices according to the four variables of agricultural intensification, and interaction terms at the block level. Variables are coded from 1 to 10, for the four simple effects (7-10) plus the six interaction effects (1-6), df: degrees of freedom of the model, logLik: log-likelihood, AICc: corrected Akaïke Information Criterion, delta: AICc difference between the model and the best model (delta-AICc<4), weight: Akaïke weight of the model (used for calculating relative importance of model parameters at the end of the model averaging procedure). Models are ranked with their AICc.

Shannon

Variables	df	logLik	AICc	delta	weight
7/8/9/10	7	-23.0837	63.7804	0	0.3611
6/7/8/9/10	8	-22.5457	65.8914	2.111	0.1257
2/7/8/9/10	8	-22.8432	66.4864	2.706	0.0933
1/7/8/9/10	8	-22.8698	66.5396	2.7592	0.0909
3/7/8/9/10	8	-22.9194	66.6389	2.8585	0.0865
4/7/8/9/10	8	-22.9515	66.7029	2.9225	0.0837
7/8/10	6	-26.0435	66.7119	2.9315	0.0834
5/7/8/9/10	8	-23.0547	66.9094	3.129	0.0755

CSI

Variables	df	logLik	AICc	delta	weight
4/6/7/8/10	8	16.0047	-11.2094	0	0.1935
6/7/8/10	7	14.326	-11.0391	0.1703	0.1777
6/7/8	6	11.7576	-8.8902	2.3192	0.0607
2/6/7/8/10	8	14.8299	-8.8597	2.3497	0.0598
7/8/10	6	11.636	-8.647	2.5624	0.0537
4/6/7/8	7	13.0709	-8.5289	2.6805	0.0507
5/6/7/8/10	8	14.6506	-8.5011	2.7083	0.05
4/7/8/10	7	12.9733	-8.3337	2.8757	0.046
2/4/6/7/8/10	9	16.2236	-8.2402	2.9692	0.0439
4/5/6/7/8/10	9	16.1648	-8.1227	3.0868	0.0413
6/7/8/9/10	8	14.3916	-7.9831	3.2263	0.0386
1/6/7/8/10	8	14.3808	-7.9617	3.2478	0.0382
4/6/7/8/9/10	9	16.0708	-7.9347	3.2747	0.0376
3/6/7/8/10	8	14.3395	-7.8789	3.3305	0.0366
1/4/6/7/8/10	9	16.0288	-7.8507	3.3587	0.0361
3/4/6/7/8/10	9	16.0178	-7.8288	3.3806	0.0357

CTI

Variables	df	logLik	AICc	delta	weight
1/4	5	40.8619	-69.9057	0	0.124
1	4	39.0637	-68.9509	0.9547	0.0769
1/4/9	6	41.5546	-68.4842	1.4215	0.0609
1/3/4	6	41.3184	-68.0118	1.8938	0.0481
1/4/7	6	41.3078	-67.9905	1.9152	0.0476
(Null)	3	37.2426	-67.7995	2.1062	0.0433
1/4/8	6	41.1488	-67.6726	2.2331	0.0406
7	4	38.3672	-67.558	2.3477	0.0383
1/4/10	6	41.0373	-67.4496	2.4561	0.0363
1/9	5	39.5942	-67.3703	2.5354	0.0349
1/7	5	39.5738	-67.3295	2.5762	0.0342
1/2/4	6	40.9434	-67.2619	2.6438	0.0331
1/4/5	6	40.9043	-67.1835	2.7222	0.0318
1/4/6	6	40.8671	-67.1092	2.7965	0.0306
1/3	5	39.3888	-66.9593	2.9463	0.0284
1/4/7/9	7	42.2139	-66.8149	3.0908	0.0264
1/10	5	39.2766	-66.7351	3.1706	0.0254
1/8	5	39.2268	-66.6354	3.2703	0.0242
1/3/4/9	7	42.1235	-66.6341	3.2716	0.0242

Variable codes: 1=Farm. prop. increase*Land. homogenisation, **2**=Farm. prop. increase*Chemic. intensification, **3**=Farm. prop. increase*Tillage reduction, **4**=Land. homogenisation*Chemic. intensification, **5**=Land. homogenisation*Tillage reduction, **6**=Chemic. intensification*Tillage reduction, **7**=Farm. prop. increase, **8**=Land. homogenisation, **9**=Chemic. intensification, **10**=Tillage reduction

CTI

Variables	df	logLik	AICc	delta	weight
4	4	37.8068	-66.4371	3.4685	0.0219
1/2	5	39.0794	-66.3407	3.565	0.0209

1/5	5	39.0769	-66.3356	3.5701	0.0208
1/6	5	39.0638	-66.3094	3.5963	0.0205
4/7	5	39.0624	-66.3065	3.5991	0.0205
1/7/9	6	40.339	-66.053	3.8527	0.0181
2	4	37.5581	-65.9397	3.966	0.0171
1/4/9/10	7	41.7744	-65.9359	3.9697	0.017
1/3/4/8	7	41.7719	-65.9309	3.9748	0.017
7/9	5	38.8654	-65.9126	3.9931	0.0168

Variable codes: 1=Farm. prop. increase*Land. homogenisation, **2**=Farm. prop. increase*Chemic. intensification, **3**=Farm. prop. increase*Tillage reduction, **4**=Land. homogenisation*Chemic. intensification, **5**=Land. homogenisation*Tillage reduction, **6**=Chemic. intensification*Tillage reduction, **7**=Farm. prop. increase, **8**=Land. homogenisation, **9**=Chemic. intensification, **10**=Tillage reduction

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