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Agricultural landscape composition as a driver of farmland bird diversity in Brittany (NW France)

Assu Gil-Tena[a,b,*], Miquel De Cáceres[b,c], Aude Ernoult[a], Alain Butet[a], Lluís Brotons[b,c,d], Françoise Burel[a]

[a] *Observatoire des Sciences de l'Univers de Rennes, UMR CNRS 6553 ECOBIO, Université de Rennes 1-UEB, Avenue du général Leclerc, Rennes Cedex 35042, France*
[b] *CEMFOR – CTFC, InForest Joint Research Unit, Solsona 25280, Spain*
[c] *CREAF, Cerdanyola del Vallés 08193, Spain*
[d] *CSIC, Cerdanyola del Vallés 08193, Spain*

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ABSTRACT

In agriculture-dominated landscapes, agricultural intensification and associated landscape homogenization have caused large declines in farmland biodiversity. This study was aimed at determining how agricultural landscape composition drives community diversity and composition of farmland birds in the characteristic *bocage* landscape in Brittany (NW France) on a broad scale. Using bird atlas data from the region (2004–2008; 10×10 km), we analyzed the importance of different components of agricultural landscape composition (types of crops, amount of semi-natural covers and elements, and artificial lands) on the alpha diversity and beta diversity of farmland birds of different functional groups, defined depending on the degree of farmland specialization and ecological requirements.

Agricultural landscape composition features explained a small amount of variation in alpha and beta diversity, particularly for specialists and residents. Cereal crops were negatively correlated with alpha diversity of all the functional groups considered whereas rotational grasslands were negatively associated with migrant and insectivorous alpha diversity. Although shrublands are not common in Brittany, they were positively associated with the occurrence of some species and particularly with alpha diversity of all the functional groups but specialists and residents. At the spatial grain of analysis, community composition was mainly driven by a gradient of alteration of the *bocage*.

To conclude, we claim for the consideration of regional idiosyncrasies in far-reaching planning schemes to prevent future biodiversity loss in agriculture-dominated landscapes due to agricultural intensification. In view of the observed large-scale trends gathered from atlas data analysis and the small amount of explained variation, we also advocate for subsequent finer scale bespoke surveys to determine the biodiversity status associated with the valuable *bocage* agricultural landscape.

1. Introduction

Both habitat heterogeneity and land-use practices influence patterns of biodiversity in agricultural landscapes (Billeter et al., 2008; Filippi-Codaccioni et al., 2010a; Fischer et al., 2011; Chiron et al., 2014). Agricultural intensification and its associated habitat homogenization have been shown to cause many detrimental effects on biodiversity in Western Europe (Benton et al., 2003). Therefore, enhancing habitat heterogeneity for biodiversity conservation is a current paradigm, which seems to depend on the degree of agricultural intensity being apparently more beneficial for high- than for low-intensity agricultural systems (Batáry et al., 2011). In addition, there is an increasing need to consider species-specific requirements which influence their response to agricultural intensity and/or landscape heterogeneity (Fahrig et al., 2011).

Spatial heterogeneity of agricultural landscapes is a result of the relative proportions and configuration of agricultural (crop) and/or semi-natural covers. Benefits of landscape heterogeneity due to the semi-natural component have already been described in many contexts (Devictor and Jiguet, 2007; Michel et al., 2007; Billeter et al., 2008; Tellería et al., 2008 but see Chiron et al., 2010;

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[*] Corresponding author at: CEMFOR – CTFC, InForest Joint Research Unit, Ctra Sant Llorenç de Morunys km 2, 25280 Solsona, Spain.
Tel.: +34 973 48 17 52; fax: +34 973 48 13 92.
E-mail address: assu.gil@ctfc.es (A. Gil-Tena).

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Filippi-Codaccioni et al., 2010b). However, additional insights into the influence of heterogeneity of agricultural covers and practices (i.e., the agricultural component of landscape heterogeneity) on biodiversity are still needed (Baudry et al., 2003; Fahrig et al., 2011) since enhancing agricultural landscape heterogeneity for preserving biodiversity without stopping crop production is a major challenge considering the increased demand for food. Alternatively, restricting human requirements for land may also be important to limit impacts on biodiversity (Phalan et al., 2011).

In Europe, declines in bird populations in the last few decades have been shown to correlate well with agricultural intensification (Chamberlain et al., 2000; Donald et al., 2001). Birds are good biodiversity indicators, having many key ecological functions (Sekercioglu, 2006; Whelan et al., 2008). The European Farmland Bird Indicator (an aggregated index of population estimates of a selected group of breeding bird species dependent on agricultural land for nesting or breeding) is considered a useful surrogate for trends in other elements of biodiversity in agricultural landscapes (Gregory et al., 2005), and is recognized as such by the European Union (Eurostat, 2012). The consideration of farmland bird responses depending on habitat breadth should add more insights to the impact of agricultural intensification and landscape homogenization on farmland bird diversity. Nevertheless, increasing awareness has been put into the need of some specialist farmland birds for large extensions of open-habitat characterized by low intensity crop systems (Filippi-Codaccioni et al., 2010a; Fischer et al., 2011; Pickett and Siriwardena, 2011; Chiron et al., 2013, 2014; Teillard et al., 2014). Agricultural intensification and landscape homogenization detrimental effects on farmland birds may also depend on migratory status (Voríšek et al., 2010; Pickett and Siriwardena, 2011), nesting strategy (Bas et al., 2009) and other ecological requirements such as breeding diet (Cardador et al., 2014, 2015).

In agriculture-dominated regions such as Brittany (NW France), biodiversity response to landscape homogenization due to agricultural intensification has been shown to be taxon-specific (Burel et al., 2004). Therefore, the assessment of farmland bird response to agricultural landscape features may provide additional insights to the fate of overall farmland biodiversity in the region of Brittany. The characteristic landscape structure in the region is the *bocage*, which is composed of a mosaic of semi-natural grasslands and crops with hedgerows in the field boundaries that play many ecological roles (Baudry et al., 2000). The *bocage* has been in regression since the second half of the 20th century because of increasing agricultural intensification, which has favored more open landscapes with a decrease in hedgerow network length, semi-natural grasslands and an increase in crop areas. Widespread crops are rotational grasslands, maize and cereals, while vegetable crops are mainly cultivated on the north-western coast.

This study aims to determine how agricultural landscape composition (mainly crops and semi-natural covers and elements) influence farmland bird diversity in the agriculture-dominated region of Brittany. For this purpose, community composition data (presence/absence) were gathered from the breeding bird atlas of the region (2004–2008; 10 × 10 km) to depict broad-scale relationships between agricultural landscape composition and avian diversity (Donald and Fuller, 1998). At the large spatial grain of analysis, hedgerow network length also represented farmland configuration and agricultural practices were not considered but are partly implicit in the different features of agricultural landscape composition such as the type of crops (e.g., arable or not, rotational or semi-natural grasslands). The considered species represent different functional groups according to their specialization and ecological requirements during the breeding season. Our specific goals were to: (1) assess the role of agricultural landscape composition as a driver of species richness of different functional groups; (2) depict farmland bird species assemblages according to agricultural landscape composition; and (3) determine the degree to which farmland bird beta diversity in Brittany is driven by agricultural landscape composition. Apart from the expected positive association with semi-natural covers and elements, at the scale of analysis we expected fewer farmland bird species with increasing homogenization of landscapes (e.g., crop dominance or type of crop) and species-specific life trait responses. We also expect a large amount of unexplained

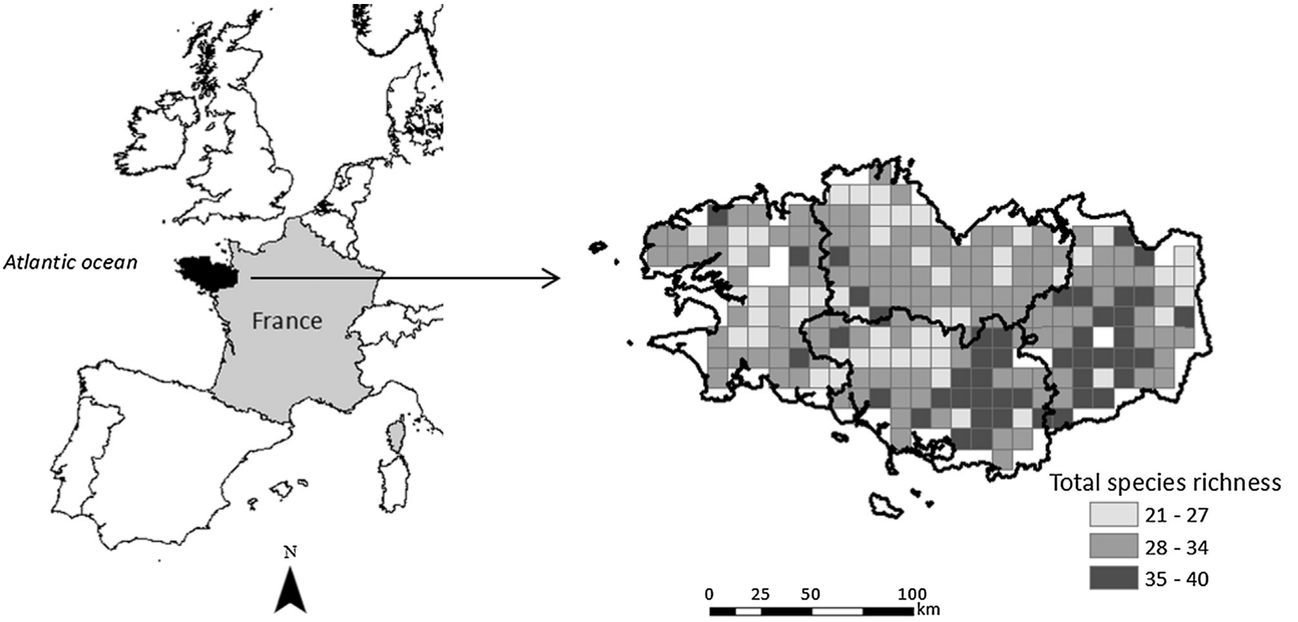


Fig. 1. Study area location (Brittany, NW France) and detail of the 223 UTM 10 × 10 km considered according to the criteria established to define agricultural landscapes (≥50% of their area is occupied by crops). Total farmland bird species richness is shown. The administrative boundaries within Brittany at the department level were also marked. From left to right: Finistère, Côtes-d'Armor (top), Morbihan (bottom) and Ille-et-Vilaine.

community composition variation, particularly taking into account the broad scale of analysis.

2. Material and methods

2.1. Study area

Brittany (27,208 km^2; Fig. 1) is a small geographical peninsula in the north-western corner of France with a long coastline along the Atlantic Ocean and a smooth relief. The region is part of the Armorican Massif and is a bedrock of shale and granite with loess deposits on the northern coast. The climate is oceanic, presenting a great spatial variability from east to west. The landscape is dominated by agriculture (60%), and forests cover just 12% of the region with heathlands only present on the shallowest soils. Impacts of agricultural intensification on this agro-ecosystem began in the 1950s and continue due to the low crop diversity of the region as well as in association with intensive farming devoted to dairy cows, pigs and poultry. Long-lasting agricultural activity may have already impacted on the avifauna diversity of the region (Devictor et al., 2010). Nevertheless, it is acknowledged that many bird species are adapted to the *bocage* landscape structure created by centuries of traditional agricultural practices (GOB, 2012) and ca. 3.5% of the terrestrial surface of the region is listed as Special

Table 1

Breeding bird species in Brittany associated with agricultural landscapes. Prevalence (percentage of 10 × 10 km sampling units occupied by each species, $n = 223$), habitat breadth and ecological traits of farmland bird species (migratory status in Brittany, ground-nesters and breeding diet). *Corvus corone*,*Erithacus rubecula*, *Fringilla coelebs*, *Parus major* and *Phylloscopus collybita* were present in the totality of the analyzed sampling units ($n = 223$) and, therefore, were excluded from the analysis. Non-migrant birds were considered as residents. The granivorous functional group was not analysed due to the low number of implied species and their high prevalence in Brittany.

Species	Acronym	Prevalence	Specialists[a]	Migrants[b]	Ground-nesters[c]	Breeding diet[d]
Accipiter nisus	ACNIS	86.16	- (other)			C
Alauda arvensis	ALARV	91.96	×		×	I/G
Anthus pratensis	ANPRA	20.09	×		×	I/G
Anthus trivialis	ANTRI	60.71	- (other)	×	×	I/G
Athene noctua	ATNOC	24.55	–			C
Buteo buteo	BUBUT	98.66	- (other)			C
Carduelis cannabina	CACAN	90.63	×			G
Carduelis carduelis	CACAR	91.52	×			G
Carduelis chloris	CACHL	97.77	- (other)			G
Circaetus gallicus	CIGAL	0.45	–	×		C
Columba palumbus	COPAL	99.55	- (other)			G
Corvus frugilegus	COFRU	16.52	×			O
Coturnix coturnix	COCOT	29.02	×	×	×	I/G
Cuculus canorus	CUCAN	88.39	- (other)	×		I
Cyanistes caeruleus	CYCAE	99.55	- (other)			I
Emberiza calandra	EMCAL	1.79	×		×	I/G
Emberiza cirlus	EMCIR	84.82	- (other)			I/G
Emberiza citrinella	EMCIT	95.54	×		×	I/G
Falco subbuteo	FASUB	67.86	–	×		C
Falco tinnunculus	FATIN	98.66	×			C
Hippolais polyglotta	HIPOL	64.29	×	×		I
Hirundo rustica	HIRUS	99.11	×	×		I
Jynx torquilla	JYTOR	2.68	- (other)	×		I
Lanius collurio	LACOL	4.46	×	×		C
Lullula arborea	LUARB	50.00	- (other)		× (*)	I/G
Motacilla alba	MOALB	91.07	×	×		I
Motacilla flava	MOFLA	3.57	×	×	× (*)	I
Numenius arquata	NUARQ	3.13	–		×	I
Oenanthe oenanthe	OEOEN	0.45	×	×	× (*)	I
Otus scops	OTSCO	0.89	–	×		I
Passer domesticus	PADOM	98.66	- (other)			I/G
Passer montanus	PAMON	11.61	×			I/G
Pica pica	PIPIC	94.64	- (other)			O
Picus viridis	PIVIR	92.41	- (other)			I
Prunella modularis	PRMOD	98.21	- (other)			I
Pyrrhula pyrrhula	PYPYR	79.91	- (forest)			G
Saxicola rubetra	SARUB	0.89	×	×	×	I
Saxicola torquatus	SATOR	83.93	×		×	I
Serinus serinus	SESER	59.82	- (other)	×		I/G
Sturnus vulgaris	STVUL	97.32	- (other)			O
Sylvia borin	SYBOR	96.43	- (forest)	×		I
Sylvia communis	SYCOM	74.55	×	×		I
Troglodytes troglodytes	TRTRO	99.11	- (other)			I
Turdus merula	TUMER	99.55	- (other)			O
Turdus philomelos	TUPHI	99.11	- (other)			O
Turdus viscivorus	TUVIS	95.09	- (forest)			I/G
Tyto alba	TYALB	61.61	×			C
Upupa epops	UPEPO	24.55	- (other)	×		I

[a] Indicates farmland specialists which were species considered within the European Farmland Bird Indicator (EFBI) in the Atlantic bio-geographical region ($n = 25$) or other specialists not included in this list (*C. coturnix* and *Tyto alba*). EFBI is an aggregated index of population trend estimates of a selected group of abundant breeding bird species dependent on agricultural land for nesting or feeding. The generalist species (represented by -) were classified according to the European Bird Census Council criteria for the Atlantic bio-geographical region (other or forest habitat) and accounting for expert criteria in Brittany (raptors and nocturnal raptors). The list of species according to the Atlantic bio-geographical region was obtained from http://www.ebcc.info/index.php?ID=491#Box%20Species%20selection%20and%20classification.

[b] Indicates true migrants in Brittany which excluded resident species and partial migratory species.

[c] Indicates species that nest on the ground; *indicates that the species nest on the ground but not exclusively in agricultural covers.

[d] Breeding diet: C is carnivorous, O is omnivorous, I is insectivorous, G is granivorous and I/G indicates a diet based on both insects and grains.

Areas of Conservation within the Natura 2000 network. In this sense, the unique agricultural landscape of Brittany is part of the Long Term Ecological Research (LTER) international network through the Armorique Zone Atelier (NE Brittany; c., 130,000 ha) characterized by a south-to-north decreasing *bocage* gradient.

2.2. Data on farmland bird community composition

Data on bird species occurrence were gathered from the Brittany breeding bird atlas (GOB, 2012). The atlas fieldwork was carried out by volunteers in 437 10 × 10 km UTM squares during the breeding period in 2004–2008. National and regional monitoring programs have also been incorporated into the fieldwork records (GOB, 2012). For the analysis, we considered data on possible, probable or certain breeding bird records. A total of 48 farmland bird species were selected (Table 1). We resorted on ornithological guides (Mullarney et al., 2000; Hume et al., 2009) and expert knowledge of the birds in the study area for species selection and subsequent functional group classification. Although the selected species widely differ in their ecological niche breadth, all of them are associated with agricultural landscapes in the studied region (i.e., species that select the *bocage* in Brittany as nesting and/or feeding substrate or in relation to other processes of their life cycle during the breeding season) and, therefore, may be impacted by agricultural intensification (Atkinson et al., 2002; Filippi-Codaccioni et al., 2010a). Excluded from analyses were: game birds, to avoid possible bias due to periodical releases for hunting purposes (e.g., *Phasianus colchicus*, *Perdix perdix*, *Alectoris rufa*); species that were recorded in the breeding atlas but in fact are accidental breeders in Brittany (e.g., *Larus ridibundus* and *Vanellus vanellus*); and species with a very restricted breeding distribution not linked to agricultural landscapes in the region but that frequent these landscapes because of great daily movement capacities (e.g., *Larus argentatus*). Moreover, some raptors were not considered since their range was not available due to their marginal distribution in Brittany and for conservation purposes (e.g., *Circus pygargus*). Species were classified according to their nesting strategy (ground nesters), type of breeding diet (e.g., insectivorous and granivorous species and strict insectivorous), migratory status [true migrants in Brittany (migrants) or not (residents; Vorísek et al., 2010)], and their degree of specialization regarding habitat extent (specialists or generalists) (Table 1). These functional categories were chosen on the basis of their different sensitivity to agricultural intensification such as in the case of ground-nesters, which were found to be more sensitive to farming intensity than hedge-nesters in France (Bas et al., 2009) or in the case of the type of breeding diet categories (Siriwardena et al., 2000; Chiron et al., 2014).

In addition to calculating the species richness in each UTM square, we also calculated the species richness of each functional group by counting the number of recorded species among those belonging to the group (Table 2). Likewise, UTM × species presence–absence tables were built for the entire bird species community and for each of the functional groups. Each of these tables was Hellinger-transformed, as recommended for community-level analyses (Legendre and Gallagher, 2001; Michel et al., 2007).

Despite the standardization work conducted during the atlas surveys and after data collection in terms of sampling effort (GOB, 2012), in subsequent analysis we considered possible sampling effort differences among the areas in which the atlas was carried out due to the differences in the amount of observations collected regarding the covered surface. For each region [Finistère (6733 km^2), Côtes-d'Armor (6878 km^2), Morbihan (6823 km^2) and Ille-et-Vilaine (6775 km^2), see Fig. 1], we considered the number of atlas observations [31,743, 28,723, 20,997 and 25,046, respectively; (GOB, 2012)] and weighted for the corresponding surface.

2.3. Agricultural landscape composition and broad-scale spatial pattern descriptors

Agricultural landscape composition was characterized by means of a remote-sensing land-use map available in the region at the spatial resolution of 250 m (i.e., 1600 pixels per 10 × 10 km UTM) and encompassing MODIS imagery from nine consecutive summer seasons (2000–2008). For each 250 m pixel, we took the statistical mode of the nine-year series (Lecerf et al., 2005, 2008) as the representative land-use for the whole period. From the identified land-use classes, we considered arable uses (differentiating maize, cereal and vegetable crops) and grassland as crops (e.g., Michel et al., 2007). Semi-natural (permanent) and rotational (managed) grasslands were differentiated. In addition, semi-natural covers were represented by forests and shrublands and the hedgerow network, which was identified from the vector geographic database BDTopo® (2003–2006) produced by the French National Geographic Institute. We also considered the area covered by artificial lands due to their association with some farmland birds and because the greater disturbance associated with urban areas that may also impact bird community of agricultural landscapes (Filippi-Codaccioni et al., 2008).

A total of 223 10 × 10 km UTM squares from the 437 sampled in the breeding bird atlas of Brittany were considered as agricultural landscapes because ≥50% of their area is occupied by crops (e.g., Atkinson et al., 2002), they were entirely situated within the administrative boundaries of Brittany and the species richness values were consistent according to their location. As agricultural landscape composition features at the 10 × 10 km resolution, we computed the area of each crop, semi-natural cover type and artificial lands, the diversity of crops and the hedgerow length (Table 2). Crop diversity at 10 × 10 km was computed as the averaged Shannon index at 1 × 1 km obtained from the proportion of each arable crops (cereal, maize and vegetables) and rotational and semi-natural grasslands (i.e., 5 crop types) regarding the total crop surface.

We aimed to avoid spurious correlations with agricultural landscape features due to large-scale factors such as climate or geology (Siriwardena et al., 2000), and/or other large-scale spatial factors affecting species distributions such as bio-geographical

Table 2
Summary statistics of the response variables (i.e., alpha bird diversity according to different ecological traits and degree of specialization; grey background) and the descriptors of agricultural landscape composition. Crops are maize, cereal, vegetable crops and grasslands.

	Mean	Min	Max	Units
Total	30.40	21	40	
Specialists	10.58	5	17	
Generalists	19.82	13	24	
Ground-nesters	4.43	1	8	
Migrants	7.72	2	15	
Residents	22.68	15	27	
Insectivorous	10.27	6	15	
Insectivorous and granivorous	7.01	4	11	
Cereal	2145	320	6851	ha
Maize	1368	129	5013	ha
Vegetables	211	6	3848	ha
Semi-natural grasslands	1766	65	4265	ha
Rotational grasslands	2655	429	5808	ha
Crop diversity	0.969	0.591	1.171	
Forests	1240	25	4435	ha
Shrublands	129	0	2393	ha
Hedgerows	437068	177073	927528	km
Artificial lands	462	19	3843	ha

constraints (Tellería et al., 2008). For this purpose, the central coordinates of the 223 10 × 10 km UTM squares [easting (X) and northing (Y)] were also taken into account because they represent the spatial structure of community composition data at broader scales than the sampling extent (i.e., linear trend in the data).

2.4. Statistical analyses

The explanatory variables were standardised to zero means and unit variances to eliminate the effect of differences in the measurement scale and sampling effort was included in all the models. Before carrying out the statistical analysis taking into account community composition and the alpha and beta diversity levels, we checked the absence of strong linear dependencies among the selected variables through bivariate correlations and variance inflation factors (VIFs).

Species richness was modeled through ordinary least squares (OLS) regression. A spatial linear detrending (X and Y coordinates) was first conducted and the residuals were then used as response variables in OLS regression. Multi model inference (MMI; Burnham and Anderson, 2002) aided in choosing the agricultural landscape composition variables that were included in the final OLS models for each response variable (Table 2). In the MMI framework, we compared alternative models with Akaike's second-order AIC corrected for small sample sizes (AICc). The selected explanatory variables for each alpha diversity variable followed averaged parameter estimates using AICc weights (AICc wi) across all OLS models per response variable accounting for all the possible combination of explanatory variables. The selected variables were significant ($p \leq 0.05$) and had an importance greater than 0.5 according to the AICc wi. Backward step-wise OLS model selection was performed to adjust the final OLS model. In addition, spatial autocorrelation of OLS model residuals was checked. In the case of detecting significant autocorrelation in model residuals, conditional autoregressive regressions (CAR) were computed to obtain spatially uncorrelated errors.

To analyze the influence of agricultural landscape composition features on farmland bird species assemblages through redundancy analyses (RDA), we first reduced the set of predictors to be used in subsequent analyses through forward selection on RDA using the UTM × species table representing the entire community as a response (Blanchet et al., 2008; Borcard et al., 2011). This procedure allowed us to assess the performance of the same set of representative predictors as drivers of community composition and beta diversity for all functional groups (see below). We computed a RDA after controlling for (i.e., partialling out) the influence of the broad-scale spatial patterns (X and Y coordinates) on species assemblages. In addition, variation in community composition (i.e., beta diversity) for the entire community and for each functional group of farmland birds was partitioned into independent components (i.e., variation partitioning; Borcard et al., 1992): pure environmental (i.e., agricultural landscape composition), pure spatial (broad-scale spatial patterns), spatial component of environmental influence (i.e., agricultural landscape composition spatially structured at a broad scale probably due to geology and/or climate) and undetermined. The relative importance of each independent component was estimated by means of percentage of explained variation in terms of adjusted R^2 (henceforth Adjusted-R^2), which accounted for the number of predictors (Peres-Neto et al., 2006).

The analysis of species richness was computed by using SAM v4.0 (Rangel et al., 2010). Multivariate analyses were performed through the "vegan" package in R (Oksanen et al., 2013), and 9999 permutations were used in all significance tests.

3. Results

Multicollinearity checking at all the biological levels of analysis ruled out semi-natural grasslands, forests and agricultural diversity in subsequent analysis due to strong correlations with the other variables and among them.

The amount of explained variation ranged from 7% (specialists) to 15% (insectivorous) in terms of Adjusted-R^2 in the OLS fitted models for farmland bird species richness ($p < 0.001$, Table 3). This result was attained after linearly detrending the response variables (Table A1 in Appendix A) and computing MMI variable selection with the obtained residuals (Table A2 in Appendix A). When accounting for spatial autocorrelation in model residuals (CAR; Table A3 in Appendix A), the models tended to be less explicative according to AICc and significant factors in the OLS models such as maize and vegetable crops and artificial areas became not significant at $\alpha = 0.05$ (see also Table 3). In any case, cereal crops did not favor species richness and rotational grasslands were negatively associated with migrant and insectivorous richness (Table 3). Although shrublands are not very common in Brittany (Table 2), they were positively related to alpha diversity of all

Table 3
Factors behind farmland bird species richness in Brittany depending on relevant ecological traits linked to agricultural intensification and degree of specialization. Ordinary least squares (OLS) backward step-wise regression was computed after selecting the explanatory variables for each response variable according to Multi Model Inference (MMI). Grey background indicates variables that were significant ($p \leq 0.05$) and had an importance greater than 0.5 according to averaged parameter estimates across 127 OLS models through MMI. In all the cases, the OLS residuals presented spatial autocorrelation ($p \leq 0.05$) and, therefore, conditional autoregressive regressions (CAR) were computed. Sampling effort has been considered at the department level within Brittany.

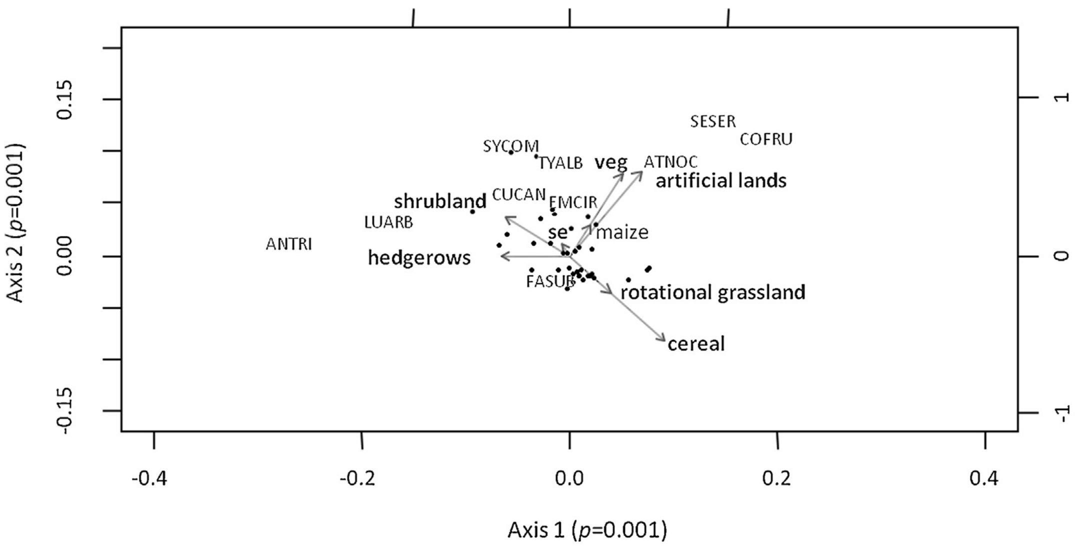
	Total	Specialists	Generalists	Migrants	Residents	Ground-nesters	Insectivorous	Insectivorous and granivorous
Model fit and significance								
Adjusted-R^2	0.11	0.066	0.116	0.151	0.081	0.147	0.081	0.093
p-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
AICc	1180.68	970.5	915.65	846.4	1002.8	763.97	723.4	779.30
Regression coefficients and significance								
Sampling effort	0.322	0.065	0.158	0.213	0.105	0.071	0.083	0.117
Cereal	−**0.936*****	−**0.478*****	−**0.554*****	−**0.359****	−**0.667*****	−**0.370*****	−**0.269****	**-0.298****
Maize	0.464*			0.235*				0.235*
Vegetables		0.344*			0.342*			
Rotational grasslands				−**0.269***			−**0.180***	
Shrublands	0.565*		**0.299***	**0.431*****		**0.346*****	**0.176***	**0.261****
Artificial lands		0.281*						

Coefficients in bold indicate the variables that remained significant at $p \leq 0.05$ after computing CAR with spatially uncorrelated errors.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.



	Axis 1	Axis 2
PIVIR	0.08	-0.01
PAMON	0.08	-0.02
PIPIC	0.06	-0.03
MOFLA	0.03	0.03
MOALB	0.02	-0.02
STVUL	0.02	-0.02
EMCAL	0.02	0.00
FATIN	0.02	-0.02
TUPHI	0.02	-0.02
COCOT	0.02	0.04
CACHL	0.02	-0.03
HIRUS	0.01	-0.02
OTSCO	0.01	0.01
PACAE	0.01	-0.02
TUMER	0.01	-0.02
ALARV	0.01	-0.02
COPAL	0.01	-0.02
TRTRO	0.01	-0.02
OEOEN	0.01	0.00
PRMOD	0.01	-0.02
PADOM	0.00	-0.03
JYTOR	0.00	0.02
SYBOR	0.00	-0.01
SARUB	0.00	0.00
TUVIS	0.00	-0.04
EMCIT	0.00	0.00
BUBUT	-0.01	-0.02
CACAN	-0.01	0.04
ACNIS	-0.01	0.04
CIGAL	-0.02	0.01
LACOL	-0.03	0.03
UPEPO	-0.03	0.09
CACAR	-0.03	0.01
SATOR	-0.03	-0.02
ANPRA	-0.05	0.10
NUARQ	-0.06	0.02
HIPOL	-0.07	0.01
PYPYR	-0.09	0.04

Fig. 2. Response of the entire community of farmland birds to the agricultural landscape composition features after controlling for the influence of broad-scale spatial patterns. Axes on the left and bottom corresponded to the species scores and axes on the right and top corresponded to the unscaled scores of the explanatory variables. To facilitate the visibility of the species ordination, many species in the central part of the figure (dots) are listed on the right, sorted in decreasing score order according to the axis 1. See the species pool and the corresponding acronyms in Table 1. Sampling effort (se) was also considered. Veg: vegetables crops.

functional groups but specialists and residents (Table 3). On the contrary, hedgerows are a characteristic linear element of agricultural landscapes in Brittany (Table 2), but at the spatial grain of analysis their effect on alpha diversity of farmland birds was not significant (see Table 3 and Table A2 in the Appendix A).

All the agricultural landscape descriptors were chosen as representative ($p < 0.01$) in the multivariate RDA forward selection and, therefore, were considered in subsequent canonical ordination analyses. After controlling for the broad-scale spatial patterns, the RDA (Adjusted-$R^2 = 0.064$, $p = 0.0001$) indicated that at the spatial grain considered (10 × 10 km) many farmland bird species were present in agricultural landscapes regardless of the intrinsic characteristics of the site (see the central portion of the RDA plot and the related species scores rightwards in Fig. 2, see also the species prevalence values in Table 1). The first canonical axis (44% of explained variation, $p < 0.001$) depicted a gradient of species associations with landscapes having diverse types and levels of human intervention ranging from those with different prevailing crops and artificial lands to those with a significant amount of semi-natural covers and elements (Fig. 2). The second canonical

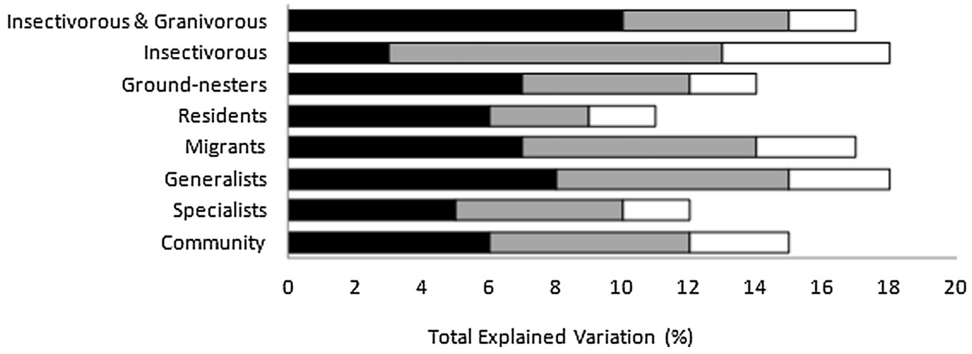


Fig. 3. Total explained variation (TEV in %) in terms of Adjusted-R^2 per functional group and contribution to farmland bird beta diversity of agricultural landscape composition (pure environmental fraction; black bar), broad-scale spatial patterns (pure spatial fraction; white bar) and the agricultural landscape composition features spatially structured at broad scale (grey bar), derived from variation partitioning analyses. RDA canonical analyses were performed considering the entire species community (Community) and the different functional groups. In all the cases, the pure fractions of the variation partitioning were significant at $p < 0.0001$.

axis (19% of explained variation, $p < 0.001$) indicated the species preference for agricultural landscapes dominated by cereal crops or by artificial lands and vegetables. Few species (e.g., *Picus viridis*, *Passer montanus* and *Pica pica*) were weakly related to cereal dominance in agricultural landscapes. Several species responded oppositely to this and were favored by the amount of complementary semi-natural habitats such as shrublands and hedgerows (e.g., *Anthus trivialis*, *Lullula arborea*, *Pyrrhula pyrrhula*, *Sylvia communis*, *Cuculus canorus*, *Hippolais polyglotta*, *Numenius arquata*, *Anthus pratensis*). *Serinus serinus*, *Corvus frugilegus* and *Athene noctua* were strongly linked to agricultural landscapes with high proportions of vegetables and artificial lands.

The total explained variation (TEV) of farmland bird community composition depicted from the variation partitioning ranged from 11% to 18% in terms of Adjusted-R^2 (Fig. 3). Residents and specialists were the functional groups attaining the smallest TEV (11% and 12%, respectively). On average, 43% of TEV was attributed to agricultural landscape composition features uncorrelated with broad-scale spatial patterns but for insectivorous (ca. 17% of TEV; Fig. 3). The spatial patterns uncorrelated with the factors considered to describe agricultural landscapes corresponded from 11% (insectivorous and granivorous) to 28% (insectivorous) of TEV.

4. Discussion

4.1. Influence of agricultural landscape composition on farmland bird community diversity

As expected, fewer farmland bird species occurred in altered *bocage* landscapes, characterised by the dominance of cereal crops and rotational grasslands and low amounts of complementary habitats such as shrublands and hedgerows. Importantly, species richness for all functional groups was negatively correlated with cereal crops. Arable crops such as cereals potentially offer nesting and foraging substrates for farmland birds but the autumn-sown associated with agricultural intensification and a subsequent tall vertical vegetation structure in the growing season may counteract the amount of available resources during the breeding season and in winter (Laiolo, 2005; Siriwardena and Hume, 2011; Cardador et al., 2014). A long-lasting agriculture activity may be also related to cereal dominance due to the more recent widespread planting of other crops such as maize during the second half of the 20th century, which was highly associated with the removal of semi-natural grasslands mainly near watercourses (Barbut and Poux, 2000). For instance, fallow areas have an acknowledged favoring role on farmland biodiversity (Siriwardena et al., 2000; Cardador et al., 2014) but used to be more abundant before the increasing use of chemical inputs linked to agricultural intensification. Therefore, agricultural landscapes with cereal dominance under intensive management practices may be an indicator of depressed availability of different nesting and foraging resources for many farmland birds. This hypothesis agrees with the associated decreases of species richness regardless of the functional group that we found in our study.

Maize crops were not a main driver of community composition and alpha diversity. Nevertheless, negative effects of maize crops on farmland bird abundance have been shown in France (Chiron et al., 2013) and Italy (Laiolo, 2005). Maize is a late crop (autumn ploughing and spring-sown) with a long period of bare soil unsuitable for breeding farmland birds. In addition, maize planting involves the removal of hedgerows and semi-natural grasslands, which also negatively impact farmland birds that make use of these habitats (Laiolo, 2005). After 1950, maize crop surface has increased from a negligible proportion to 400,000 ha in Brittany (Barbut and Poux, 2000). Therefore, although at the spatial grain of analysis the expectable negative effect of maize on farmland birds was not observed, this cannot be excluded at the population level, particularly considering the delayed response of farmland birds to agricultural intensification (Chamberlain et al., 2000).

A positive effect of grasslands on farmland bird diversity would be expectable (Joannon et al., 2008; Chiron et al., 2013; Teillard et al., 2014) but the strong negative correlation among semi-natural grasslands and the different arable crops and forests precluded to disentangle their role on farmland bird diversity in our analyses. Rotational grasslands were negatively correlated with insectivorous and migrant species. Management intensity has also been shown to impact farmland bird diversity at smaller scales (Batáry et al., 2007). Rotational grasslands are usually sown and fertilized, which favors a poor vegetation composition and decreases the associated invertebrate diversity and abundance (Vickery et al., 2001). Therefore, the increased proportion of rotational grasslands in Brittany (Table 2) as in other regions of Western Europe (Chamberlain et al., 2000; Vickery et al., 2001) seems to already have impacted some sensitive farmland birds at broad scale.

The positive effect of shrublands on species richness of some functional groups may be due to their low disturbance level, their role as a complementary habitat in agricultural landscapes for foraging purposes (Fuller et al., 2004) and because some species also use this habitat for nesting (e.g., *Emberiza cirlus*, *H. polyglotta*, *Lanius collurio*, *Prunella modularis*, *S. communis*). Together with shrublands, hedgerows were also drivers of community composition positively associated with some farmland birds. More than 200,000 km of hedgerows have been removed in Brittany during the second half on the 20th century (Barbut and Poux, 2000). This may have negatively affected particular groups of farmland birds such as non-ground-nesters (Bas et al., 2009; Batáry et al., 2010). In addition, hedgerow network length enhanced farmland bird diversity in simple agricultural landscapes with depressed amounts of semi-natural covers in Germany (Batáry et al., 2010). The lack of effect of hedgerow network length on the alpha diversity modeling may be partly linked to the fact that, at the spatial grain of analysis, hedgerows are linear landscape elements more associated with landscape configuration than composition. At smaller spatial grains of analysis, weaker relationships have been found between landscape configuration and farmland bird patterns compared to landscape composition features (Picket and Siriwardena, 2011). Moreover, at our scale of analysis we did not take into account hedge management and quality which may seriously vary according to the type of crop or pasture dominance (see Batáry et al., 2010 and references therein). Some species (e.g., *A. trivialis*, *L. arborea*, *P. pyrrhula*, *C. canorus*) may also use other semi-natural habitats such as forest patches (Fuller et al., 2004) but we could not study their effect due to the strong negative correlations with arable crops and the positive association with semi-natural grasslands. Nevertheless, many farmland birds may not correlate with them, particularly specialists which have been shown to be strongly dependent on a dominance of either arable crops or grasslands (Teillard et al., 2014).

Agricultural landscapes with vegetable crops and artificial lands were also drivers of community composition and positively correlated with the presence of a few farmland birds. Human habitation may increase farmland bird community variation in the particular case of species like *Tyto alba*, *S. serinus*, *Sturnus vulgaris*, *Hirundo rustica*, but not affect alpha diversity of farmland birds as previously shown by Filippi-Codaccioni et al. (2008). The role of vegetable crops on farmland bird diversity is still uncertain although the population of some species (e.g., *C. frugilegus*) may be favored by them due to their vertical vegetation structure in the growing season, feeding or nesting substrate availability (Siriwardena and Hulme, 2011).

Our results partially support the hypothesis that heterogeneous agricultural landscapes improve farmland bird species richness

(Benton et al., 2003) since a dominance of cereal crops did not improve richness. Crop diversity at 10 × 10 km was not considered in further analyses due to the high positive association with maize (*rho* = 0.70). Moreover, a more informative crop diversity measure would be the one with more types of arable crops but this was not possible at the land cover map resolution. Increased species richness in farmlands has been associated with high diversity of agricultural covers and less intensive agriculture in France (Devictor and Jiguet, 2007; Doxa et al., 2010). At a finer spatial grain, mixed habitats with a significant amount of semi-natural grasslands have been shown to be crucial in the positive response of kestrels (*Falco tinnunculus*) to land-use changes after agricultural intensification and crop expansion in Brittany (Butet et al., 2010). Nevertheless, the most specialist farmland birds usually require a certain degree of local habitat simplification such as large patches of extensive crops (e.g., Filippi-Codaccioni et al., 2010a; Fischer et al., 2011; Pickett and Siriwardena, 2011; Teillard et al., 2014), which could not be modeled at the spatial grain considered here.

The large amount of unexplained community composition variation was probably due to the atlas spatial grain and because community level analysis usually entails weak results in terms of explained community variation even when considering fine-scale spatial patterns (Gilbert and Bennett, 2010). Nevertheless, we cannot discard low associated avian beta diversity in Brittany probably due to the long-lasting agriculture activity (Devictor et al., 2010). The small amount of explained variation by the broad-scale spatial factors alone (i.e., uncorrelated with agricultural landscape composition) may be associated with other environmental factors not considered in the analysis and biotic processes such as dispersal constraints (Legendre and Legendre, 1998). Veech and Crist (2007) showed that beta diversity among landscapes was mainly determined by environmental heterogeneity within a region and less so by dispersal limitation. Other unconsidered factors behind beta diversity of farmland birds could be agricultural practices (Chiron et al., 2014), any land cover providing landscape matrix heterogeneity (e.g., wetlands) and habitat (Devictor and Jiguet, 2007) or microclimate divergences.

The response of the species assemblages depended on the functional group. As expectable ground-nesters were mainly specialists (Table A4 in Appendix A) but the former responded more to agricultural landscape composition which agrees with Bas et al. (2009) when comparing farmland bird abundance responses to spatial variation in agricultural production intensity according to nesting strategy and habitat specialization. Ground-nesters were also more insectivorous and granivorous dependent (Table A4 in Appendix A), which may explain the similar modeling performance and the factors affecting both functional groups. Migrants significantly tended to be insectivorous (Table A4 in Appendix A) and agricultural landscapes with more migrants had also more species of strict insectivorous (Table A5 in Appendix A). This may be due to the fact that insectivorous species are mainly non forest specialist (Table 1) and may be limited by feeding substrate westwards in Brittany (Table A1 in Appendix A) where forests are more abundant (Wretenberg et al., 2010). Specialist species richness positively correlated more with residents (Table A5 in Appendix A) in spite of no significant species traits correlation (Table A4 in Appendix A) or clear broad scale spatial patterns response (Table A1 in Appendix A). This agrees with the lack of correlation with complementary habitats such as shrublands for both functional groups. The low predictive power of our models for these two functional groups indicates the need to study them at finer spatial grains of analysis, and in the case of residents a year-round basis approach should be also considered in order to reflect annual resource availability. Modeling may improve in the case of specialists if species' farmland habitat preference regarding arable crops and grasslands is also considered (Teillard et al., 2014).

4.2. Study limitations and outreach

We are aware that our inferences are limited because most farmland management is carried out at a finer scale than our spatial grain of analysis. Other scales of analysis and subsequent descriptors of agricultural landscape composition, configuration and practices are therefore required to study the determinants of farmland bird diversity in detail. Nevertheless, the availability of the Brittany breeding bird atlas, the environmental data and our analytical approach allowed us to extract coarse-grained drivers of farmland bird diversity in the agriculture-dominated landscapes of Brittany, one of the uses of atlas data (Donald and Fuller, 1998). We acknowledge that the low crop diversity and the uniqueness of the *bocage* landscape structure in Brittany pose some limits to the generalization of our results to other regions. Higher crop diversity may be expected at finer spatial scales in homogeneous agriculture-dominated landscapes and, particularly, when the temporal crop sequence was considered, with positive effects on farmland biodiversity as shown in other parts of France (Joannon et al., 2008). Our results may be probably only applicable to other regions of NW Europe or even NW France with similar cultural landscapes and patterns of avian diversity due to strong landscape homogeneity associated with agriculture (Devictor et al., 2010). Nevertheless, the utility of atlas data to depict broad scale trends of farmland bird diversity is valuable regardless of the geographic range. In this sense, some of the discussed hypotheses can be assessed at finer scales. In addition, unraveling the relative influence of landscape homogenization and intensive agricultural practices will be also envisaged (Chiron et al., 2014).

5. Conclusions

In agriculture-dominated regions with intensive farming activity such as Brittany, large extensions of intensive managed crops do not provide a favorable structure for breeding or nesting substrates required by many farmland birds and different functional groups. Therefore, the widespread dominance of crops such as cereals and rotational grasslands in contraposition to undisturbed semi-natural covers (shrublands) is a major concern due to the subsequent alteration of the characteristic *bocage* landscape structure and the increasing surface of the former crops or others such as maize (Houet et al., 2010). Our results show the consequences for local biodiversity of agricultural policies determined centrally by the authorities (e.g., Common Agricultural Policy in the EU) without considering regional idiosyncrasies (Chiron et al., 2013). In Brittany, two of the main types of farming systems may have different impacts on bird community composition in farmlands in an indirect way. Rotational grasslands largely devoted to dairy production in the region were associated with less migrant and insectivorous farmland bird species whereas the dominance of cereal crops for pig and poultry production was associated in general with fewer farmland birds. In addition, in Brittany, pig and poultry production largely depends on imported feedstuffs (e.g., soybean, manioc) and, therefore, the impacts on biodiversity could span elsewhere (Baudry et al., 2010), eventually impacting more Brittany agroecosystems such as in the case of increasing nitrogen pollution because of livestock manure. To conclude, large-scale monitoring programs at the regional scale such as the Brittany breeding bird atlas have been shown to be effective tools to assess farmland bird responses to agricultural landscape composition, despite the need to conduct further research at smaller scales through bespoke surveys.

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Appendix A.

See Tables A1–A5.

Table A1
Alpha diversity linear detrending per functional group. The sign of the regression coefficient is shown in brackets.

	Adjusted-R^2	Easting	Northing
Total	0.09	(+)**	(−)**
Specialists	0.04	(+)**	(−)
Generalists	0.12	(+)*	(−)***
Migrants	0.27	(+)***	(−)***
Residents	−0.006	(+)	(−)
Ground-nesters	0.066	(+)	(−)**
Insectivorous	0.26	(+)***	(−)***
Insectivorous & granivorous	0.17	(+)***	(−)***

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

Table A2
Averaged variable importance and significance obtained through AICc weights in the MMI across 127 OLS models. For each response variable, explanatory variables are ordered by increasing importance. Sampling effort was always considered.

Response variable (AICc)	Explanatory variable	Importance	t
Total (1183.2)	Sampling effort	1	1.197
	Cereal	1	−4.155
	Shrublands	0.803	2.732
	Vegetables	0.669	2.785
	Maize	0.569	2.831
	Artificial lands	0.39	2.793
	Hedgerows	0.369	−2.613
	Rotational grasslands	0.273	−0.98
Specialists (969.8)	Sampling effort	1	0.589
	Cereal	0.967	−3.058
	Vegetables	0.824	2.75
	Artificial lands	0.713	2.708
	Maize	0.548	2.817
	Shrublands	0.546	2.825
	Rotational grasslands	0.461	2.757
	Hedgerows	0.396	−2.65
Generalists (919.6)	Sampling effort	1	1.431
	Cereal	1	−4.34
	Shrublands	0.835	2.745
	Rotational grasslands	0.601	−2.81
	Maize	0.364	2.607
	Vegetables	0.326	2.504
	Artificial lands	0.286	−1.469
	Hedgerows	0.274	−1.345
Migrants (850.2)	Sampling effort	1	1.685
	Shrublands	0.996	3.633
	Cereal	0.981	−3.227
	Rotational grasslands	0.826	−2.761
	Maize	0.76	2.732
	Vegetables	0.34	2.627
	Artificial lands	0.335	2.428
	Hedgerows	0.271	−0.066
Residents (1006.8)	Sampling effort	1	0.792
	Cereal	0.999	−4.144
	Vegetables	0.765	2.746
	Hedgerows	0.475	-2.871
	Rotational grasslands	0.44	2.842
	Artificial lands	0.331	2.369
	Maize	0.317	2.192
	Shrublands	0.294	2.043
Ground-nesters (764.7)	Sampling effort	1	0.969
	Cereal	0.998	−3.92
	Shrubland	0.998	3.78
	Maize	0.703	2.756
	Artificial land	0.552	−2.82
	Rotational grasslands	0.377	−2.619
	Vegetables	0.312	−2.374
	Hedgerows	0.279	0.99
Insectivorous (727.0)	Sampling effort	1	0.689
	Cereal	0.978	−3.166
	Shrublands	0.846	2.736
	Rotational grasslands	0.593	−2.821
	Maize	0.509	2.839
	Artificial lands	0.437	2.803
	Vegetables	0.358	2.716
	Hedgerows	0.269	−0.361
Insectivorous & granivorous (783.0)	Departament	1	1.098
	Cereal	0.973	−3.133
	Shrublands	0.89	2.796
	Maize	0.834	2.733
	Rotational grasslands	0.39	−2.753
	Vegetables	0.374	2.775
	Hedgerows	0.335	2.334
	Artificial lands	0.27	−1.088

Table A3
CAR computed for the models in Table 3 with spatially autocorrelated residuals. Only the model fit attributed to agricultural landscape composition predictors is shown (Adjusted-R^2).

	Total	Specialists	Generalists	Migrants	Residents	Ground-nesters	Insectivorous	Insectivorous and granivorous
Model fit and significance								
p-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
AICc	1188.1	979.4	920.04	852.6	1009.3	768.43	726.8	787.89
Regression coefficients and significance								
Sampling effort	0.28	0.113	0.267	0.216	0.235	0.119	0.081	0.173
Cereal	-1.19^{***}	-0.489^{***}	-0.623^{***}	-0.409^{***}	-0.663^{***}	-0.454^{***}	-0.284^{***}	-0.364^{**}
Maize								
Vegetables								
Rotational grasslands				-0.271^{*}			-0.181^{*}	
Shrubland			0.292^{*}	0.356^{**}		0.335^{***}	0.161^{*}	0.21^{*}

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

Table A4
Mean square contingency coefficient (Phi coefficient) among the species functional traits (degree of specialization and ecological requirements), ($n = 48$, see Table 1).

	Specialists	Generalists	Migrants	Residents	Ground-nesters	Insectivorous
Generalists	–					
Migrants	0.13	−0.13				
Residents	−0.13	0.13	–			
Ground-nesters	0.39^{**}	-0.39^{**}	0.05	−0.05		
Insectivorous	0.04	−0.04	0.47^{***}	-0.47^{***}	0.05	
Insectivorous & granivorous	0.10	−0.10	−0.15	0.15	0.44^{**}	-0.45^{**}

** $p < 0.01$.
*** $p < 0.001$.

Table A5
Pearson correlations among the alpha diversity response variables. All the correlations were significant at $p < 0.001$.

	Total	Specialists	Generalists	Migrants	Residents	Ground-nesters	Insectivorous
Specialists	0.873						
Generalists	0.858	0.499					
Migrants	0.830	0.683	0.757				
Residents	0.878	0.802	0.715	0.462			
Ground-nesters	0.743	0.676	0.609	0.678	0.600		
Insectivorous	0.806	0.706	0.689	0.860	0.543	0.617	
Insectivorous & granivorous	0.847	0.657	0.814	0.771	0.685	0.822	0.637

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