Effects of non-cropped landscape diversity on spatial dynamics of farmland birds in intensive farming systems

François Chiron [a,*], Ondine Filippi-Codaccioni [a], Frédéric Jiguet [a], Vincent Devictor [b]

[a] Muséum national d'Histoire naturelle, Conservation des Espèces, Restoration et Suivi des Populations, UMR 7204 MNHN-CNRS-UPMC, CP 51, 55 rue Buffon, 75005 Paris, France
[b] Institut des Sciences de l'Evolution, UMR 5554 CNRS-UM2, Université Montpellier 2, Place Eugène Bataillon, 34095 Montpellier cedex 05, France

A B S T R A C T

Increasing habitats diversity in agricultural landscapes has been proposed as a key measure for reversing the decline of farmland biodiversity in Europe. However, indicators used for assessing such a potential compensation effect usually only rely on species diversity and abundance while ignoring variations in species-specific vulnerability. The extent to which habitat diversity may reverse the decline of specialist species in Europe to farming systems is thus still unclear. In this study, we investigate whether the effect of non-cropped habitat diversity on farmland birds' occurrences was dependent on species' specialization for habitats. In particular, we focused on the relative effects of non-cropped habitat diversity on species' abilities to persist or to colonize new vacant areas. We used a capture–recapture statistical framework to study the spatial dynamics of 20 farmland bird species in France monitored from 2001 to 2007. We found that non-cropped landscape diversity reduces both the probabilities that a species becomes extinct locally and that a species colonizes new vacant areas, and the occupancy rate. Although this suggests a possible stabilizing effect of the surrounding habitat diversity on species occurrence in farming systems, the occupancy was only weakly affected. Moreover, we found that the most specialist species were the more negatively affected by this landscape diversity in terms of colonization abilities. We argue that accounting for the differences in habitat specialization among farmland species can improve conservation policies dedicated to the management of landscape diversity.

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1. Introduction

An increasing amount of literature provides evidence that landscape diversity can mitigate biodiversity loss in intensive agricultural contexts (Roschewitz et al., 2005; Tscharntke et al., 2005; Rundlöf et al., 2008). Enhancing diversity of farmland has thus been proposed as a key measure for reversing the decline in farmland biodiversity across Europe (Benton et al., 2003). These evidences are mainly based on analyses using either species richness or species abundance, these two metrics being considered as good indicators of biodiversity fate. But limiting approaches to the use of abundance and richness for assessing the importance of landscape diversity on the conservation of farmland birds may impair our ability to definitively address the question tackled by Benton et al. (2003) in a specific review on this issue: is heterogeneity the key? Actually, to address this question, one should go beyond the measurement of species number or abundance to look at species-specific traits and the eventual impacts on community structure and composition. Species are not equally at risk when facing global changes (Julliard et al., 2004). Adopting a trait-based approach can shed light on the

driving forces of biodiversity loss (MacGill et al., 2006; Jiguet et al., 2007; Devictor and Robert, 2009; Bas et al., 2009). For instance, a recent study showed that bird species specialists to farmland habitats in France are more abundant in fields surrounded by homogeneous landscapes than in mixed landscapes composed of arable, forest and urban areas, and regardless of the farming intensity (Filippi-Codaccioni et al., 2010a). In another study, arable fields within intensive agricultural landscapes with little non-crop area can support a similar diversity in cereal aphid parasitoids than structurally complex landscapes (Vollhardt et al., 2008), suggesting that these organisms may find necessary resources even in simple landscapes. Hence, making generalisations regarding the relationship between landscape diversity and biodiversity in arable fields appears difficult without looking at species-specific habitat requirements (Filippi-Codaccioni et al., 2010b).

In this paper, we explored the relationship between the responses of farmland bird species to landscape diversity and their habitat specialization in intensive agricultural lands. We focused on the effect of the non-cropped diversity as it has been shown to deeply affect richness and stability of bird assemblages (Devictor and Jiguet, 2007). Devictor and Jiguet (2007) showed a positive relationship between species richness, community stability, and the diversity of non-cropped habitats. This process has however

not been investigated at the population level and the influence of species' specialization level on population dynamics has yet to be explored. Especially, we do not know if the diversity of non-cropped habitats at the landscape scale influence occurrence and stability of farmland bird populations themselves. Recent work suggested that some farmland specialist bird species really need relatively large open landscapes and could be negatively affected by habitat diversity such as trees and bushes (Filippi-Codaccioni et al., 2010b). But whether it holds true for all species occurring in farmland is unclear as some of them are dependent on smaller patches of suitable habitat and are therefore much less likely to be affected by landscape level habitat diversity. This could have great implications for the conservation of farmland birds at the level of landscape.

Measuring species' fates in human-modified environments is most usually investigated using static variables such as local abundance, or species occurrence, in given areas, whereas species dynamics (i.e., local extinction and colonization events) is rarely considered. Since Devictor and Jiguet (2007) suggested that farmland bird communities could be influenced by source–sink dynamics, we adopted a dynamic approach and tested the effects of non-cropped landscape diversity on the occurrence, and the rates of extinction and colonization events for farmland bird species. Understanding population changes spatially is of central interest in ecology but has rarely been applied to conservation purposes (MacKenzie et al., 2006). Yet, spatial approach could provide supplementary insights in the functioning of populations facing global changes (Altwegg et al., 2008).

We presume that the ability of farmland birds to colonize and maintain local populations along a gradient of non-cropped habitat diversity will depend on their habitat specialization level. In particular, we predict that an increase in the diversity of non-cropped habitats in intensive arable landscapes will modify habitat conditions for farmland specialists in nesting and feeding. An increase in the non-cropped diversity could reduce capacities of specialized species to colonize vacant areas and increase local vacancy of sites previously occupied (local extinction). On the contrary, increase in the diversity of non-cropped habitats will provide new patches of habitats providing supplementary resources around fields, potentially increasing local settlement of generalist species to a site not previously occupied (local colonization). Although difficult to verify, we assumed that the colonization of a mosaic of non-cropped habitats by generalist species could also be a consequence of the relaxed competition from specialist species negatively affected by the degradation of the cropped habitats. Finally, following the assessment of the role played by non-cropped habitat diversity on the population dynamics of farmland birds, we make a number of general assertions on population functioning facing habitat diversity (Hanski, 1999; Gaston and Blackburn, 2002).

As bird detection may vary in space and time, we used site occupancy models as developed by MacKenzie et al. (2003) for correcting all estimates by the detection probability of individual species. Occupancy studies usually deal with one single species (Chiron et al., 2008; Martin et al., 2009, but see Kéry et al., 2009). Here we worked on 20 species to show the complexity of species responses to land-use in agricultural landscapes, using count data on common breeding birds collected in France from 2001 to 2007 within the national Breeding Bird Survey scheme.

2. Methods

2.1. Bird survey

The French Breeding Bird Survey (FBBS) is a standardized monitoring program in which volunteer skilled ornithologists identify breeding birds by song or visual contacts each spring. Each observer

is allocated a locality, and a 2×2 km^2 plot to be surveyed is randomly selected within a 10-km radius around this locality. Such random selection ensures that the survey covers a representative selection of habitats (including intensive farmland, ordinary forest, suburbs and cities). Each plot is monitored twice in the spring, once before and once after the 8th of May, with 4–6 weeks between sampling events. In each plot, the observer carries out 10 evenly distributed point counts, within which the observer records every species heard or seen during a 5-min period. The same observer monitors the same plot each year at similar dates and hours (Julliard and Jiguet, 2002). During the 2001–2007 study period, we analysed all BBS plots surveyed which 10 points are located in farmland as defined by the Corine Land Cover database (see landscape variables below). We selected the 10 point counts of each plot and deduced the presence of each species at the point level when the species was detected at least once during the two annual visits.

Previous studies have shown that the FBBS was able to reflect large spatial and temporal trends including quite fine relationships between landscape or climatic characteristic and population dynamics (Devictor et al., 2009; Jiguet et al., 2007; Julliard et al., 2006).

2.2. Habitat specialization and selection of species

Using the same French BBS data, Julliard et al. (2006) defined an index of habitat specialization using the variation of abundance among various habitat classes for a given species. They grouped habitat categories in 18 homogeneous habitat classes, and provided a simple measure of specialization for a given species by calculating the coefficient of variation (the standard deviation divided by the mean) of the abundance of the populations across habitats (Julliard et al., 2006). The species specialization index (SSI) was estimated for the 105 most frequent terrestrial bird species using all FBBS plots surveyed at least once between 2001 and 2004 ($n = 1022$). This measure allows the ordering of species from specialists (more abundant in few habitat classes) to generalists (more uniform abundance across habitat types), lower values of SSI being attributed to the more generalist species and higher values to the more specialist species. Previous analyses have shown that the specialization index (SSI) was neither biased by taxonomic autocorrelation nor by small sample size (Devictor et al., 2008), and that it is congruent with other metrics developed to estimate habitat specialization (Reif et al., 2010). Note however that if specialization level was, by construction, dependent on habitat diversity, our conclusions could be circular. Fortunately, the SSI was shown to be independent from habitat heterogeneity (Devictor et al., 2007).

Among the 105 bird species most recorded by the BBS, we used a list of 20 bird species derived from the Farmland Bird Index (Gregory et al., 2005) and adapted to France. Although these species all breed in farmland environments, some of them also exploit non-cropped areas for feeding and nesting, like wastelands, bushes, planted trees or woody habitats (e.g. warbler species like the whitethroat or the melodious warbler, and finches like the Goldfinch or the Linnet, Table 1). As a result of our selection, the index of species specialization (SSI) to farmland habitats varies among species, with values ranging from 0.40 to 2.23. For comparison, the SSI's values of the 190 most common species in France ranges from 0.2 to 3.8 (Julliard com. pers.). So our selection enabled us to analyse variations in the response of species to landscape diversity with relatively high power and was not biased to the most specialist species on farmland.

2.3. Landscape variables and diversity estimates

We obtained variables related to landscape features within each surveyed plot using the geographical information system package

Table 1
Number of plots where species occurrence was either detected (or not) over the country. Naïve occupancy (not corrected by the detection probability) is compared to true estimated occupancies (estimated from a simple parameterization with only occupancy and detection, NS, non-significant, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$, NC, no model convergence).

Species	Species presence	2001	2002	2003	2004	2005	2006	2007	Total number of plots	Naive occ.	SE	Estimated occ.	SE	Difference (p-value)	SSI-value
Skylark	Non-detected	2	14	21	32	34	42	35	180	0.81	0.03	0.84	0.04	**	1.16
	Detected	33	52	113	126	143	142	139	748						
Tawny Pipit	Non-detected	32	64	128	152	170	178	169	893	0.04	0.01	0.03	0.02	NS	2.00
	Detected	2	2	6	6	7	6	5	34						
Meadow Pipit	Non-detected	27	50	98	124	147	155	143	744	0.20	0.03	0.39	0.06	***	1.37
	Detected	8	16	36	34	30	29	31	184						
Tree Pipit	Non-detected	22	45	97	95	103	103	96	561	0.40	0.03	0.32	0.06	***	0.91
	Detected	13	21	37	63	74	81	78	367						
Linnet	Non-detected	7	17	38	57	65	82	78	344	0.63	0.03	0.81	0.05	***	0.70
	Detected	28	49	96	101	112	102	96	584						
Goldfinch	Non-detected	9	15	30	45	64	64	76	303	0.67	0.03	0.86	0.06	***	0.70
	Detected	26	51	104	113	113	120	98	625						
Common Quail	Non-detected	28	56	117	132	132	147	147	759	0.18	0.03	0.17	0.05	***	1.52
	Detected	7	10	17	26	45	37	27	169						
Cirl Bunting	Non-detected	26	48	101	118	136	144	139	712	0.23	0.03	0.30	0.05	***	0.59
	Detected	9	18	33	40	41	40	35	216						
Yellowhammer	Non-detected	9	19	29	44	50	50	51	252	0.73	0.03	0.76	0.05	*	0.71
	Detected	26	47	105	114	127	134	123	676						
Melodious Warbler	Non-detected	19	38	73	84	80	80	81	455	0.51	0.03	0.41	0.06	***	0.72
	Detected	16	28	61	74	97	104	93	473						
Red-backed Shrike	Non-detected	29	50	110	123	133	147	138	730	0.21	0.03	0.25	0.05	*	1.24
	Detected	6	16	24	35	44	37	36	198						
Corn Bunting	Non-detected	20	43	83	101	110	109	111	577	0.38	0.03	0.37	0.05	NS	1.46
	Detected	15	23	51	57	67	75	63	351						
White Wagtail	Non-detected	18	30	53	64	62	89	80	396	0.57	0.03	0.58	0.07	NS	0.69
	Detected	17	36	81	94	115	95	94	532						
Yellow Wagtail	Non-detected	12	34	80	91	103	113	102	535	0.42	0.03	0.50	0.06	***	2.09
	Detected	23	32	54	67	74	71	72	393						
Northern Wheatear	Non-detected	31	64	120	139	159	162	163	838	0.10	0.02	0.12	0.05	*	1.70
	Detected	4	2	14	19	18	22	11	90						
Whinchat	Non-detected	33	63	125	149	170	177	168	885	0.05	0.01	NC	NC	***	1.70
	Detected	2	3	9	9	7	7	6	43						
Stonechat	Non-detected	21	32	73	83	102	109	100	520	0.44	0.03	0.53	0.06	***	0.78
	Detected	14	34	61	75	75	75	74	408						
Turtle Dove	Non-detected	8	20	37	55	57	59	61	297	0.68	0.03	0.72	0.07	**	0.40
	Detected	27	46	97	103	120	125	113	631						
Whitethroat	Non-detected	5	21	41	47	60	64	57	295	0.68	0.03	0.74	0.06	***	0.65
	Detected	30	45	93	111	117	120	117	633						
Lapwing	Non-detected	33	60	125	143	163	165	157	846	0.09	0.02	0.13	0.05	***	2.23
	Detected	2	6	9	15	14	19	17	82						

ArcView 3.2 (ESRI, 2000) and the Corine Land Cover database (CLC). The latter is a national geo-referenced database including the main habitats for the whole country in contiguous polygons classified into 44 different land-cover categories (Bossard et al., 2000). We overlaid FBBS plots on CLC database and we built two groups of explanatory variables: habitat cover and landscape diversity variables (Devictor and Jiguet, 2007). More specifically, the 44 land-cover categories were grouped into six main habitat types in order

to select landscape types which were both relevant to test predictions on bird community, and compatible with a landscape scale investigation. These six main habitat types contain three agricultural main habitats: (i) intensive agricultural land which includes large open fields of annually harvested plants and irrigated cultures as well as permanent crops such as vineyards and olive groves; (ii) extensive agricultural land, which includes small farmlands generally growing non-permanent crops (arable land
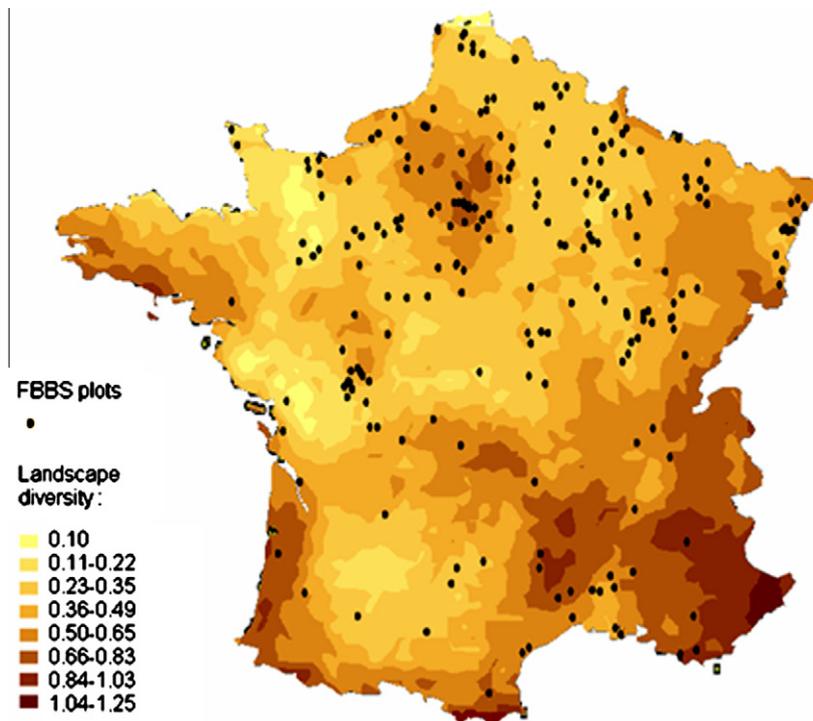
Fig. 1. Non-cropped landscape diversity across France. Each dot represents a plot monitored between 2001 and 2007 by participants in the French Breeding Bird Survey (n = 227).

or pastures); (iii) pasture, as farmland used mainly for grazing but which could also be mechanically harvested. The other three non-farmland habitats were categorised as: (iv) woodland, (v) scrub (which included natural moors and transitional woodland) and (vi) artificial land covers (cities, villages, roads …). FBBS plots could contain different kinds of these habitat types. As we were mainly interested in the compensation effect of non-cropped habitats diversity in intensive agricultural plots, we further selected FBBS plots which share intensive agricultural land (the first category defined above (i), for a total of 227 plots) and no extensive one (categories (ii) and (iii)). Thus, every point count was associated to this type of intensive agriculture.

We calculated the proportions of artificial lands (i), the proportion of semi-natural habitats based on all polygons covered by woodlands and bushes (iv and v), and the proportion of arable lands based on polygons of intensive agricultural lands (i) within the 227 plots. We calculated the diversity of non-cropped habitats (Landiv) within plots using the Shannon's diversity index (Fig. 1) based on all polygons of any non-intensive agricultural habitat types (i.e., all categories except (i)), and the diversity of cropped habitats based on all polygons of intensive agricultural lands among the 44 land-cover categories (Devictor and Jiguet, 2007).

2.4. Occupancy and dynamics estimates

To estimate site occupancy by farmland species, while taking species detection probability into account, we used the likelihood-based method developed by MacKenzie et al. (2003). This method is based on the framework of the closed-population mark-recapture analysis. Closure means that, during the sampling period, the occupancy state of a site is assumed to be constant. Within a breeding season, the logic is that temporally repeated observations of a closed system provide the information to enable separation of non-occurrence from non-detection. From successive surveys of a pool of study sites over years, underlying processes of farmland species occupancy (site-extinction and site-colonization probabilities) can then be estimated on the basis of the robust design (Pollock, 1982). Usually, robust design is restricted to mark-recapture studies with temporal replicates. Here we use a space-for-time substitution approach and consider the 10 sampling points of a FBBS plot as secondary sampling replicates (Chiron et al., 2008). From 2001 to 2007, the visit each year to FBBS plots represented the primary sampling occasions (n = 7 years).

We used the default parameterization of MacKenzie et al. (2003) as we are mainly interested in describing local extinction and local colonization along a gradient of landscape diversity. Using the notation of MacKenzie et al. (2003), the estimated true occupancy at year 1 (ψ_1) is the probability that a given FBBS plot is occupied by a species in 2001 and (p_1) is the probability to detect a species given their presence during one secondary sampling occasion (i.e., one sampling point within a plot). Let (εt) be the probability that a plot occupied at year t become vacant at $t + 1$ (local extinction) and (γt) be the probability that a plot vacant at year t is occupied by the species at $t + 1$ (local colonization).

2.5. Modelling and selection of models

Species detection history is modelled through a series of probabilistic parameters (see MacKenzie et al., 2003). An important assumption of this modelling technique is parameter constancy (i.e., detection and occupancy should not vary among plots). However, the influence of plot-specific covariates likely to induce diversity in those parameters can be included in the model. Occupancy, extinction, colonization, and detection for a given habitat were thus modelled as a logistic function of the continuous variable landscape diversity (Landiv) in a multiple-season model. Initially, we also included the species specialization index as a continuous covariate to test its effect on spatial parameters and detection directly in the framework of the model. Although this procedure of modelling was a rather simple approach, models including the

species specialization index (SSI) as a variable had surprisingly high deviance and provided estimates with large error values so that we decided to model the effect of species specialization separately. We modelled occupancy, extinction, colonization, and detection as a function of the landscape diversity and of the categorical variable 'Species' (SP) distributed in 20 supplementary factors in the structure of each model, each corresponding to one bird species.

A number of models were then fitted to the data that, step by step, constrained all parameters to be constant among the 7 years, as well as along landscape diversity (Landiv) gradient. Models were ranked using Akaike's information criterion (AIC; Burnham and Anderson, 2002), which allows selection of the most parsimonious model from a candidate set. Models with the lowest AIC, and AIC differences of less than 2, have a substantial level of empirical support and yield estimates that are relatively similarly precise and unbiased (Burnham and Anderson, 2002). Model fitting, estimating, and testing were carried out with the program MARK (White and Burnham, 1999).

For best models showing differences in occupancy, extinction and colonization probabilities among farmland bird species, we compiled species parameter estimates and tested the correlation between parameter estimates and species specialization. For best models showing an interaction between the species and the landscape diversity, we tested for a relationship between the level of species specialization and the direction and the strength of the species' responses, i.e., the slope between species extinction (and colonization) and the landscape diversity. We used linear model (after logarithmic or exponential transformation to allow normality in the distribution of data) with species response as the dependent variable and the species specialization as the independent variable. Linear model enabled us to weight each species response by the inverse of its variance to account for uneven precision of the slope estimate among species. We performed statistical analyses with the R statistical software version 2.6.1 (R Development Core Team, 2004).

3. Results

3.1. Species detectability

Model selection suggested that detectability was not constant among species between 2001 and 2007 (Table 2). Overall, the probability of detection varies from 0.10 for the Northern Wheatear to 0.51 for the Skylark (mean estimates (SE) = 0.27 (0.01)) and is not correlated with the species specialization index (SSI) (Pearson's $r = -0.39$, $p = 0.11$). At the plot level, proportion of plots occupied by farmland species that were calculated from the detection and the non-detection histories (i.e., naïve estimates) led to underestimation of true occupancies (i.e., corrected) for most species (Table 1). Accounting for imperfect detection allows us to avoid potential biases when assessing the relationship between spatial estimates and species specialization index.

3.2. Effects of non-cropped landscape diversity on spatial dynamics of birds

After accounting for imperfect detection of species, model selection indicated that both local occupancy and events of local extinction and local colonization, are not randomly distributed among plots and/or among species (Table 2; the weight of the model $\{\psi(\cdot)\varepsilon(\cdot)\gamma(\cdot)p(\cdot)\} \sim 0$ gives little support for constancy in parameters). Based on the AIC values, model selection suggested that local extinction, local colonization and the resulting local occupancy are functions of species and non-cropped landscape diversity (Table 2). Derived from estimates obtained with model 1, the mean probability of local occupancy (and associated standard error SE), the mean probability of local extinction (SE) and the mean probability of colonization to a site not previously occupied (SE) were 0.41 (0.05), 0.12 (0.04) and 0.09 (0.04), respectively. Using model 1 estimates, we further showed that non-cropped landscape diversity had negative effects on both probabilities of local extinction and local colonization, but also on local occupancy rate of farmland species (mean slopes (SE) were -0.15 (0.12), -0.41 (0.11) and -0.26 (0.16), respectively). Model selection also suggested that effects of non-cropped landscape diversity on extinction and colonization varied among species: there was support for models with local extinction and colonization as a function of 'Species' interacting with 'Landscape diversity' (Table 2).

3.3. Interactions between the landscape diversity, the proportion of habitat types and the species specialization index

Based on the compilation of these estimates (from model 1), we then assessed the strengths and the directions of the relationships between local extinction, colonization and occupancy and the species specialization index (SSI) (Fig. 2a–c). There was no relationship

Table 2
Summary of model selection procedure results for the occupancy (for 2001) and related parameters for the farmland birds. Data are issued from the French Breeding Bird Survey covering the country from 2001 to 2007. Models are supported by biological hypothesis and ranked according to Δ.

No.	Models[a]	Δ	w	np	Hypotheses
1	$\psi(\text{SP} + \text{Landiv})\varepsilon(\text{SP} \times \text{Landiv})\gamma(\text{SP} \times \text{Landiv})p(\text{SP} \times \text{Landiv})$	0.0	0.95	141	Effects of landscape diversity and species on occupancy, extinction and colonization
2	$\psi(\text{SP} + \text{Landiv})\varepsilon(\text{SP} \times \text{Landiv})\gamma(\text{SP} + \text{Landiv})p(\text{SP} \times \text{Landiv})$	6.1	0.05	122	Effects of landscape diversity and species on occupancy, extinction and colonization
3	$\psi(\text{SP})\varepsilon(\text{SP} \times \text{Landiv})\gamma(\text{SP} \times \text{Landiv})p(\text{SP} \times \text{Landiv})$	13.2	0.00	140	Effects of landscape diversity and species on extinction and colonization and of species on occupancy
4	$\psi(\text{SP} + \text{Landiv})\varepsilon(\text{SP} + \text{Landiv})\gamma(\text{SP} \times \text{Landiv})p(\text{SP} \times \text{Landiv})$	18.8	0.00	122	Effects of landscape diversity and species on occupancy, extinction and colonization
5	$\psi(\text{SP} \times \text{Landiv})\varepsilon(\text{SP} \times \text{Landiv})\gamma(\text{SP} \times \text{Landiv})p(\text{SP} \times \text{Landiv})$	41.5	0.00	160	Effects of landscape diversity and species on occupancy, extinction and colonization
6	$\psi(\text{SP} + \text{Landiv})\varepsilon(\text{SP} \times \text{Landiv})\gamma(\text{SP} \times \text{Landiv})p(\text{SP} + \text{Landiv})$	248.3	0.00	122	Effects of landscape diversity and species on occupancy, extinction and colonization
7	$\psi(\text{SP} \times \text{Landiv})\,p(\text{SP} \times \text{Landiv})$	4274.8	0.00	80	No extinction and no colonization
8	$\psi()\varepsilon(\cdot)\gamma(\cdot)p(\cdot)$	6324.2	0.00	4	Extinction and colonization are random events
9	$\psi(\text{Landiv})\varepsilon(\text{SP} \times \text{Landiv})\gamma(\text{SP} \times \text{Landiv})p(\text{SP} \times \text{Landiv})$	No convergence			Effects of landscape diversity and species on extinction and colonization and of landscape diversity on occupancy

[a] Factors affecting occupancy (ψ), extinction (ε), colonization (γ) and detection (p) probabilities include the species (SP) and the non-cropped landscape diversity (Landiv). Given are the relative difference in AICc values compared to the top-ranked model (Δ), AICc weights (w) and the number of parameters (np) in various models of farmland birds dynamics.
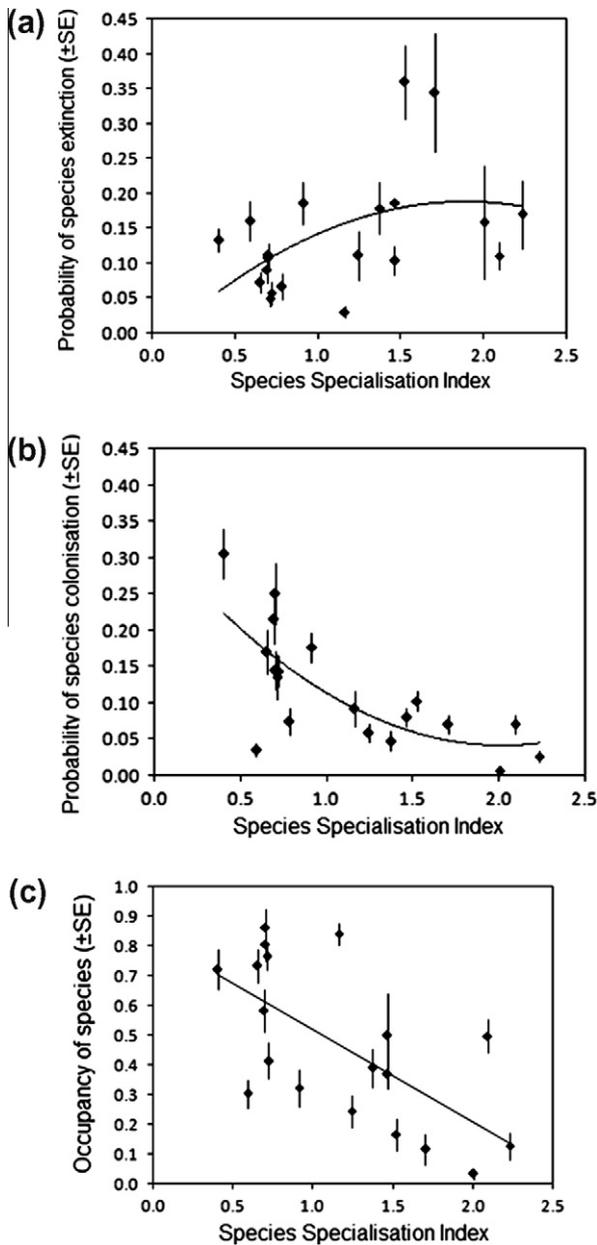
Fig. 2. Relationships (a) between the probability of local extinction of farmland species in 2×2 km^2 plots ($n = 227$) and the specialization index (SSI), (b) between the probability of local colonization and the specialization index and (c) between the probability of local occupancy and the specialization index. Each dot represents one species ($n = 19$). We removed the whinchat from the figure because the model did not converge. We used data from the FBBS from 2001 to 2007. Relationships are issued from model 1 estimates presented in Table 2.
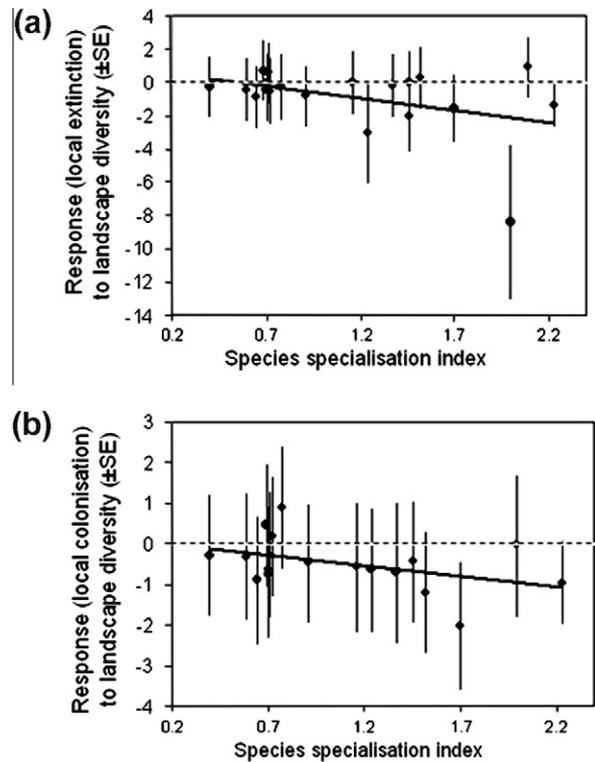

Fig. 3. Spatial responses of farmland bird species in term of (a) the probability of local extinction and (b) the probability of local colonization to the landscape diversity measured in 2×2 km^2 plots ($n = 227$) along a the gradient of species specialization. Each dot represents one species ($n = 18$). We removed the whinchat from the figure (a) and the whinchat and the yellow wagtail from the figure (b) because the model did not converge. We used data from the FBBS from 2001 to 2007. Relationships are issued from model 1 estimates presented in Table 2.

between local extinction and species specialization ($R^2 = 0.02$, $p = 0.60$), but a trend for a negative relationship between local colonization and species specialization ($R^2 = 0.19$, $p = 0.06$) as well as a negative relationship between local occupancy and species specialization ($R^2 = 0.56$, $p < 0.001$). Finally, we assessed the relationship between species' responses, i.e., the slope between local extinction (and local colonization) and landscape diversity for each species, and the species specialization index (SSI) (Fig. 3a and b). We removed the whinchat and the yellow wagtail from the species' colonization responses (Fig. 3b) because the model did not converge. There was no correlation between species' extinction responses and SSI values ($R^2 < 0.01$, $p = 0.82$), but a negative relation-

ship between species' colonization responses and SSI values ($R^2 = 0.23$, $p = 0.04$).

Interestingly, there was no correlation between the diversity of cropped habitats and the diversity of non-cropped habitats within the 4 km^2 plots (Rho Spearman = 0.004, p-value = 0.943). This shows that these two factors are independent dimensions of the landscape. Finally, we noted positive correlations between the diversity of non-cropped habitats and both the proportion of forest areas (mean value = 0.21) (Rho Spearman = 0.39, p-value < 0.001), and areas of urban patches (mean value = 0.07) (Rho Spearman = 0.45, p-value < 0.001) within plots. However there was no correlation between the non-cropped habitat diversity and the proportion of cropped area (mean value = 0.70) (Rho Spearman = −0.06, $p = 0.44$) within plots.

4. Discussion

We investigated the role played by the diversity of non-cropped habitats on population dynamics and site occupancy of farmland birds. We first found that the non-cropped landscape diversity within the 400 ha plots had a negative effect on both the local extinction and the local colonization of farmland bird specialists. In other words, non-cropped landscape diversity had a stabilizing effect on population dynamics. It is likely that a mosaic of different non-farmed habitats provides a diversity of resources, such as refuges and feeding areas, and hence stabilizes bird populations of a majority of farmland bird species through time by increasing their chances to persist on sites previously occupied, with no further need to later re-colonize these sites. This stabilizing effect was previously only shown at the community level (Devictor and Jiguet, 2007).

We further tried to disentangle the relative effects of the colonization and the extinction processes on the occurrence of species locally. Obviously, we did not expect the spatial dynamics of bird populations at the scale of a patch of vegetation to be perfectly stable as individuals naturally face local extinction and local colonization events (e.g. due to stochastic processes and source–sink dynamics). But more interestingly, we found that the apparent effects of non-cropped habitat diversity on these two processes did not balance each other in our study. Though bird populations better persisted in plots with higher habitat diversity than in plots with a lower diversity, their chances to settle in new vacant plots also decreased more rapidly along the same gradient. Therefore, the reduction in colonization events could not compensate site vacancy in high habitat diversity context. As a consequence, species occupancy, which is a parameter resulting from extinction and colonization dynamic processes, also decreased along a gradient of decreasing non-cropped habitat diversity. These results thus suggest that farmland birds disappear from heterogeneous non-cropped landscapes in France due to their poor ability to colonize new intensive agricultural sites. Our results emphasize that in intensive farmland landscapes, spatial dynamics of birds within farmland also depend on the habitat diversity found in adjacent patches.

In our case, because we used data on birds within FBBS plots that were available at a 2×2 km^2, we analysed the diversity of non-cropped habitats at this scale only and not at a more detailed resolution. It should be noted that our results may differ according to the spatial resolution as suggested by multi-scale analyses that measured the effect of landscape structure on bird richness in various types of habitats (Clergeau et al., 2001; Heikkinen et al., 2004). To our knowledge, spatial responses of specialist and generalist species to habitat diversity are unknown at broader and at smaller scale resolution than 400 ha. So it would be interesting to examine whether our results hold true at a different spatial resolution. However, we note that our results are consistent with findings of a recent study showing a positive effect of homogeneous arable landscapes (measured within 12 ha plots) compared to mixed ones on the abundance of the most specialist birds to farmland habitats (Filippi-Codaccioni et al., 2010a).

Because we used a limited number of factors for modelling the response of the 20 farmland species to landscape diversity, the effect of the non-cropped diversity on the dynamics of birds could have masked effects of other key factors like the diversity of cropped habitats and appearance of specific habitats (i.e., the relative proportion of each habitat within plots). In fact, the cropped and the non-cropped diversities were not correlated each other, so it is unlikely that the diversity of cropped habitats explains our results. However, semi-natural habitats and artificial landcovers contributed significantly to increase habitat heterogeneity but did not reduce the amount of intensive agricultural lands.

Our second important finding is that population dynamics of a given species depends on the species-specific traits, here the habitat specialization level. We first found no distinction in extinction responses to surrounding non-cropped habitat diversity between more and less specialized birds. However, our results suggest that the more specialized the birds, the lower their ability to colonize new cropped patches when breeding close to more diverse non-farmland habitats. This result shows that even in a community principally composed of farmland species, contrasts in colonization processes exist between species according to their level of specialization. A possible explanation could be the increasing competition between specialist and generalist species, the latter being more able to benefit from fragmented habitats (so called fine-grained environment, Levins, 1968). Generalist species could therefore nest and feed on more numerous resources in a diverse landscape, therefore maintaining a better meta-population dynamics. More diverse non-cropped habitats may also be less attractive than very open landscape to farmland specialist species because of an increase of predation pressure on field margins (Newton, 1998). Farmland specialist birds are usually ground nesting species compared to generalist ones that often nest on hedgerows and bushes (Bas et al., 2009). So, specialist species may tend to avoid breeding closed to high features such as trees and wood edges to limit predation due to the presence of a higher number of carnivores (red foxes, mustelids and cats), or raptors (owls) that shelter and breed on field margins in mixed landscapes, compared to generalist ones. Alternatively, the detected effects of landscape diversity on the spatial dynamics of farmland birds could only result from the reduction of cropped area in more heterogeneous landscapes, impacting population viability through reduced population size. However, we found no correlation between cropped area and non-cropped diversity. We are therefore confident that our results reflect the specific effects of non-cropped habitat diversity and not simply the trivial consequence of the removal of cropped area within plots. Furthermore, as we corrected the estimates by the probability of detecting the species, our result cannot simply result from a possible lower detection probability of more specialized species in more diverse non-cropped areas.

Although our results are only based on data collected in intensive farming systems, it is likely that they confirm both theoretical and experimental findings of many previous studies on the decline of specialist species in farmland (Siriwardena et al., 1998; Chamberlain and Fuller, 2000; Donald et al., 2001; Gregory et al., 2005), in intensive farming systems (Bas et al., 2009), but also in various types of habitats (Owens and Bennet, 2000; Marvier et al., 2004; Julliard et al., 2006; Devictor et al., 2008). These findings suggest that species which relate the most on restricted habitats (and/or resources) are the most affected by the perturbation and degradation of these particular habitats (or resources) (Krauss et al., 2003).

The investigation of differential responses among species according to an ecological trait in terms of population dynamics leads to further insight into the possible effects of the management of landscape diversity in intensive cropped landscapes. Indeed, while habitat diversity at both farm and landscape levels has been previously reported to improve farmland species diversity and abundance (Benton et al., 2003), as well as species richness and community stability (Devictor and Jiguet, 2007), our results suggest a possible negative effect of the landscape diversity on the most specialized species in terms of population dynamics. Therefore, the possible compensation effect of landscape diversity in homogeneous and intensive farmland landscapes, as recently proposed by Roschewitz et al. (2005) and Tscharntke et al. (2005), could not benefit to those highly specialized species. Moreover, if diversity-enhancing agri-environmental schemes should target lowland bird populations, it is likely that they do not favour farmland specialist species, albeit being the species facing greater population depletions. We thus suggest that designing landscape management and priority areas for farmland-specialized birds should be achieved according to the differences between more or less specialist species to thrive in farmlands.

5. Conclusion

We showed that extensive non-farmed areas that surround intensively farmed fields in an agricultural landscape matter. We suggest that the future of farmland birds depends on how the complete matrix is managed (Norris, 2008), including not only agricultural habitats, but also the wider landscape including semi-natural, natural and artificialized habitat patches. Our conclusion does not support the benefit of enhancing non-cropped habitat diversity

within intensive farming landscapes but the necessity of maintaining landscape structure homogeneous with large surface of open fields in order to maintain populations of birds nesting in agricultural landscapes and especially the most specialized species to farmland habitats. To this regard, our results are in accordance with the concept of land sparing management of agricultural landscapes that aim at separating patches of remnant nature from cultivated areas for conserving farmland bird diversity (Green et al., 2005; Fischer et al., 2008).

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