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RESEARCH ARTICLE

Land sharing or land sparing? Implications for farmland birds of conservation concern in France

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Abstract
Purpose Farmland bird populations have experienced widespread declines across Europe, raising urgent questions about how agricultural landscapes should be structured to reconcile biodiversity conservation and food production. Land sparing and land sharing represent two contrasting strategies, yet empirical evidence remains mixed.
Objectives We aim to quantify responses of bird communities along a land sharing–sparing gradient and identify which landscape management strategies best support different ecological groups.
Methods Using the French Breeding Bird Survey, we analyzed 810 locations monitored between 2001–2024. A land sharing–sparing gradient was quantified using forest area, agricultural heterogeneity, and landscape diversity indices. Bird counts were modeled with negative binomial spatio-temporal Bayesian models (`INLA`), incorporating climate, spatial random fields, and temporal autocorrelation.
Results Forest specialists responded positively to greater forest area, supporting land sparing. Generalists benefited from higher agricultural heterogeneity, consistent with land sharing. Unexpectedly, farmland specialists did not benefit from increased heterogeneity, and conservation-priority farmland species showed negative associations with natural elements.
Conclusion No single land-use strategy maximizes abundance across all bird groups. Land sparing favors forest specialists and conservation-priority species, while land sharing benefits generalists. Context-dependent landscape planning and customized agricultural practices are essential.

Keywords Land sharing and land sparing · Farmlands birds · INLA · Conservation

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Introduction

With the current global biodiversity decline (Burns et al. 2021; Inger et al. 2015), land use allocation is a major challenge for biodiversity conservation. Agricultural landscapes are central to this issue, as they cover a large proportion of European territory and harbour a substantial part of biodiversity.

Several studies show that farmland bird populations are declining in Europe (Donald et al. 2001; Bowler et al. 2019). This decline is mainly explained by the intensification of agricultural practices (Rigal et al. 2023; Genty et al. 2026) and pesticide use (Monnet et al. 2026; Perrot et al. 2025). Heldbjerg et al. (2018) also shows that ground-nesting birds are in significant decline in Denmark whereas birds nesting elsewhere are less impacted. This raises the question of how land should be allocated to maximize biodiversity. Two main land-use strategies are commonly discussed (Fischer et al. 2014; Grass et al. 2019; Fahrig 2020, 2013): land sparing and land sharing. The land sparing approach separates highly intensive agricultural production from conservation areas in order to minimize trade-offs between food production and biodiversity preservation. In such landscapes, agricultural areas are typically characterized by large, homogeneous patches and intensive farming practices, which often result in low biodiversity. In contrast, biodiversity is concentrated in relatively large protected areas such as national nature reserves or forests. By contrast, the land sharing approach aims to support both food security and biodiversity by promoting their coexistence within the same landscapes. These landscapes are generally composed of many small agricultural fields interspersed with trees, hedgerows, or semi-natural elements. As a result, they tend to be more heterogeneous, with higher connectivity between habitat patches, and farming practices are usually less intensive.

Today, there is no consensus on how to allocate land use to maximize biodiversity and agricultural output. Indeed, on the one hand Phalan et al. (2011) and Edwards et al. (2015) show that land sparing is better to conserve biodiversity in Ghana, India and Colombia. On the other hand, Riva and Fahrig (2022) show that small patches contain higher diversity. Moreover, Lamb et al. (2019) show that land sparing would more likely only benefit forest birds and would disadvantage farmland birds in the United Kingdom. Finch et al. (2019) proposes a solution based on three compartments enabling some large forest patches to conserve woodland birds, some low-intensity agriculture to conserve farmland birds and some big fields to ensure food security.

These previous results suggest that the effect of land sharing or land sparing on bird abundance depends on both the landscape and species' needs. These needs correspond to the ecological niches of the species, which may be narrow for specialist species and broader for generalists (Devictor et al. 2010).

To resolve this uncertainty in the French agricultural landscapes, which covers more than half the country with highly diverse farming practices (Nagy and Soós 2025), we need robust monitoring approaches. Birds serve as ideal indicators of biodiversity because they are easy to sample, cover a wide range of life-history traits, are present in all habitats (even in intensively farmed areas) and trophic levels (Padoa-Schioppa et al. 2006; Aghababyan 2024), and are sensitive to environmental stressors (Canterbury et al. 2000; Gregory et al. 2003; Rigal et al. 2023). Moreover, the high availability of bird data from participatory science makes it particularly well-suited to address questions on land use allocation.

Additionally, citizen science facilitates bird data collection because many volunteers are skilled at bird identification. Hence, thanks to thousands of skilled French birdwatchers we gathered an extensive database from a breeding bird survey called the French Breeding Bird Surveys (Jiguet et al. 2012; Fontaine et al. 2021).

As indicators of land sharing and land sparing are complex, we need to take into account many variables that structure the landscape and bird populations. Moreover, to account for the spatio-temporal structure, a Bayesian framework and inference with `INLA` (Rue et al. 2009) appears to be particularly suitable because it efficiently handles the hierarchical structure of spatio-temporal data with multiple covariates.

In this study, we use spatio-temporal Bayesian modeling to disentangle the effects of land sharing and land sparing scenario on bird populations, with a focus on farmland and forest birds and particularly on species of conservation concern. We formulated the following hypotheses:

1. Land sharing is expected to benefit generalist and farmland species. In land-sharing landscapes, the

higher diversity of habitat patches may provide a wider range of nesting opportunities for generalist species. For farmland species, lower agricultural intensity under land sharing is predicted to promote breeding success and survival.

2. Land sparing is expected to benefit forest species, particularly those of conservation concern. Forest specialists are generally sensitive to human disturbance; therefore, larger contiguous areas allocated to biodiversity conservation under land sparing are predicted to enhance their abundance.

Materials and methods

Data

Bird abundance data

The data are provided by the French Breeding Bird Surveys (Jiguet et al. 2012; Fontaine et al. 2021). It aims to survey the common French breeding bird populations over time and space in France. This is a participatory program where thousands of skilled volunteers will count birds. These volunteers get randomly assigned a 2 km by 2 km square, next to the place they live, by the French National Museum of Natural History. Once this square is assigned, the volunteer needs to choose ten evenly distributed points inside the square (at least 300 m apart). Then, each year the volunteer has to visit the square twice during breeding season to record bird abundance. A visit of the square consists of staying 5 min at each point and recording every seen or heard bird (Jiguet et al. 2012).

In order to obtain clean data, we removed all squares that were not surveyed at the required dates and times, as well as squares containing fewer than ten observation points (approximately 2% of the data). We considered two sources of detectability bias Nabias et al. (2024): the probability that individuals present actually make themselves detectable, and the probability that the observer successfully detects them. To reduce these biases, we aggregated all points within each square and retained the maximum abundance recorded across the two visits. Aggregating data at the square scale also makes statistical analysis using INLA computationally feasible.

To have enough temporal depth in our analysis we only kept time series of at least five years. As our goal is to study the effect of different kinds of agricultural practices on bird population, we removed all squares that have three or more points classified as urban by the observer or at least 25% of urban land use in the square.

It left us with a total of 810 squares that have been observed at least five years in a row. We used the French Breeding Bird Surveys classification (Fontaine et al. 2021) of bird to categorize birds with their main types of habitat adding two species to agricultural birds: *Passer montanus* (Barlow et al. 2020) and *Burhinus oedicnemus* (Hume et al. 2020).

To disentangle the effects of land sharing and land sparing on French bird populations, we divided birds into groups of habitat specialization (agricultural, forest and generalist birds) given by Fontaine et al. (2021) and Julliard et al. (2006). Then, we used the French IUCN list (France et al. 2016) to classify the species in two categories: least concerned and birds with conservation concern. In the French IUCN list (France et al. 2016) they mention birds for which the category changes between 2008 and 2016. As our dataset goes from 2001 to 2024, we considered that a species is with conservation concern if it is not "least concerned" in 2008 or 2016.

Maps of distribution of birds' observation by group are shown in Supplementary material Section 1 (Fig. SI-1 for generalist species, Fig. SI-2 for forest species, Fig. SI-3 for agricultural species, Fig. SI-4 for forest species with conservation concern and Fig. SI-5 for agricultural species with conservation concern).

Environmental data

Climate data is taken from WorldClim (Harris et al. 2020). For each square and year we retrieved minimum and maximum temperatures and total amount of precipitation of the previous spring (March to June) as well as minimum and maximum of previous summer (July and August). Minimum and maximum temperatures are preferred over mean temperature as they better capture extreme events such as heatwaves and cold snaps that are known to affect bird reproduction (Thepault et al. 2025). Then we added the latitude of each site, mean-centered across all study sites (such that positive values indicate sites north of the mean latitude of the dataset, and negative values indicate sites south of it). This allows us to account for the interaction between spring temperature and site conditions as in Thepault et al. (2025) (by using latitude as a proxy of historical temperature condition of the site), and provides a validation check by testing whether our model recovers the same interaction effect on reproductive success.

We used CORINE Land Cover (CLC) (Land 2018) to retrieve land cover variables. This database contains all land uses in France in a raster format (grain size is 100 m) for years 2000, 2006, 2012 and 2018. The different kinds of land uses are described in 44 groups (Section 5 of Supplementary material). For each year, we retrieved in each square the surface of agricultural (CLC class "Agricultural areas", codes starting by 2), forest (CLC class "Forest", codes starting by 31), natural (CLC classes "Shrubs and/or herbaceous vegetation associations" and "Open spaces with little or no vegetation", codes starting by 32 or 33), water (CLC classes "Wetlands" and "Water bodies", codes starting by 4 or 5) and artificial (urban) lands (CORINE class "Artificial areas", codes starting by 1). This provides a general assessment of the use of each square. We did a linear interpolation of the data when it was not constant between two years of data.

Land sharing and sparing indicators

To create indicators of land sharing and land sparing, we took the intersection of CORINE patches with a disk of radius 10 km centered on each square. This landscape-scale window, larger than the 2 km square itself, is motivated by the fact that land sharing and sparing patterns emerge at the scale of entire agricultural landscapes rather than individual fields Grass et al. (2019).

This allowed us to obtain, for each square, the number of patches intersecting the disk, their area within the disk and their type. As the area of forest around the square is a great indicator of land sparing we retrieved the total area of forest patches intersecting a disk of 10 km radius around the center of the square (without any distinction between different forest types).

Then, we used as a variable the area of the CLC class "Land principally occupied by agriculture, with significant areas of natural vegetation" (code 243) in the disk around each square. We call this variable agriculture with a significant amount of nature in the following. This variable is an indicator of wildlife friendly agriculture and thus a land sharing indicator.

Finally, to have an indicator of the heterogeneity of agricultural practices, we computed a Shannon index (Shannon 1948) on agricultural land uses around the squares where the "species" is the kind of agricultural patch and the abundance the number of each kind of agricultural patch (CLC class "Agricultural areas", codes starting by 2). Shannon's index thus reflects the diversity of farming practices around each square, rather than overall landscape diversity. If this index is high then there is a high diversity in land uses, saying we are more in a land sharing scenario. Otherwise, it means that we are in a monocultural scenario meaning that we are in a land sparing scenario. An example of the land use around a square is given in Fig. 1.

To conclude this part a higher forest area implies a land sparing scenario whereas a higher amount of agriculture with significant amount of nature or a higher Shannon index implies a land sharing scenario.

Correlation study and principal component analysis (PCA) on the land cover variables

The land use of each square consists of five highly correlated variables (forest, agricultural, water, artificial and natural area in the square defined in Section "Environmental data") as they all sum up to the area of the square (4 square kilometers). We therefore applied a PCA to reduce these variables to a smaller set of uncorrelated components. After computations, we can summarize land use variables into the first three components of the PCA explaining 80.8% of the variance of the data (Fig. SI-7c). The axes are represented in Figs. SI-7a and SI-7b. The first axis, called $PC_{agri/forest}$, separates the agricultural squares (negative) from the natural and forest squares (positive). The second axis, called PC_{urban}, separates urban (and water) squares (positive) from the others. The third axis, called PC_{open}, separates closed squares (forest and cities) from the open squares (flat lands). Table SI-1 shows the PCA loadings of land use of the square onto these axes. In the following, we will use these three variables to represent landscape at the scale of the square.

We present in Table SI-2 a correlation matrix of the other variables we use hereafter.

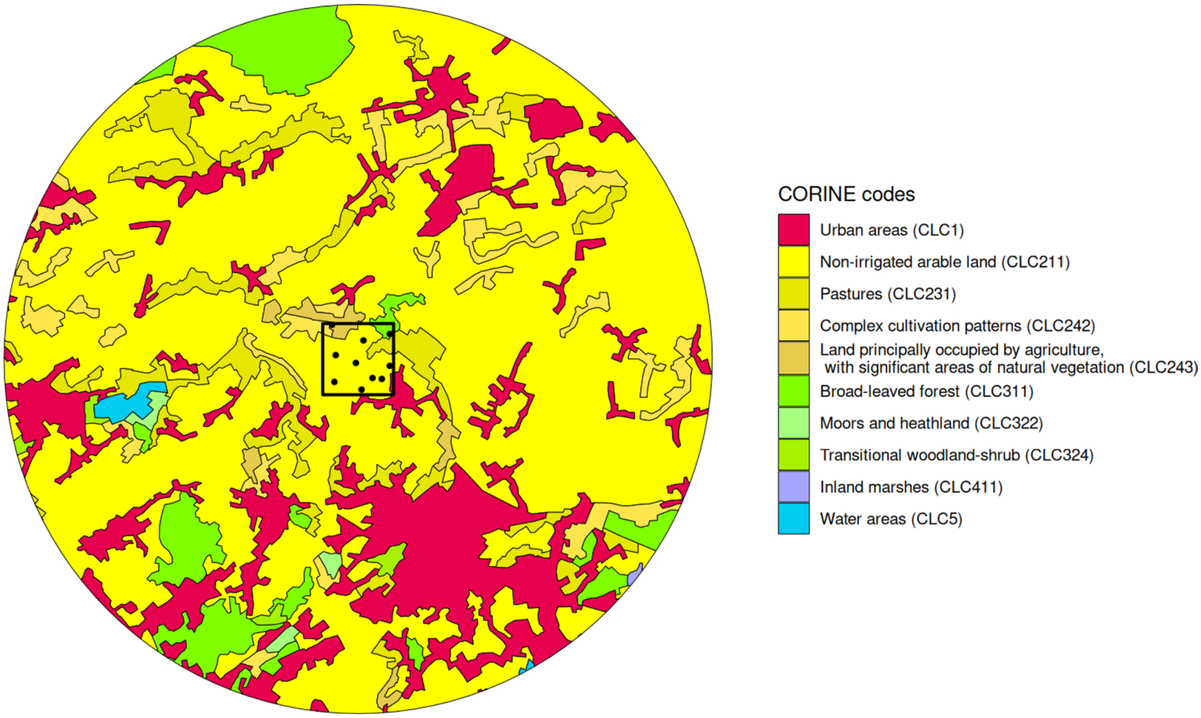

Fig. 1 Example of the land use in a 10 km radius disk around a square (black line). Each color represents a different kind of land use following the table in Supplementary material Section 5 (colors used are the official CORINE colors). Shannon's indices are calculated only with agricultural patches (codes starting with a two). In this case there are 68 agricultural patches spread in four categories. The black dots represent ten points of samples

Statistical approach

Model

Bird abundance may vary due to multiple drivers such as land-use change, climate variability, agricultural practices, and interactions with other species. To quantify these effects, we modelled bird counts using a negative binomial regression model, which accounts for overdispersion in the data due to aggregation of counts within the same square, and other sources of extra variability in bird count data. Formally, if p is the number of covariates, the expected abundance at location s and year t is defined as:

$$\log \lambda(s,t) = \beta_0 + \sum_{k=1}^{p} \beta_k X_k(s,t) + \sum_{i=1}^{p} \sum_{j=i+1}^{p} \beta_{i,j} X_i(s,t) X_j(s,t) + w_{s,t},$$

where $X_k(s,t)$ denote environmental covariates (e.g. climate, land cover), and $w_{s,t}$ represents residual spatio-temporal variability. Interaction terms, $X_i(s,t)X_j(s,t)$, allow us to capture non-additive effects between environmental drivers. In our case, we used the separable case for the spatio-temporal variability:

$$w_{s,t} = w_s + w_t,$$

where w_t is an autoregressive model and w_s is a Matérn random field. For the temporal effect, there is a correlation between years, modelled in the following way:

$$w_t = \phi w_{t-1} + \epsilon_t,$$
$$\epsilon_t \sim \mathcal{N}(0, \tau^{-1}),$$

where ϕ is the auto-correlation parameter and τ is the precision parameter. For the spatial Matérn random field, the covariance is as follows (as in Krainski et al. (2018)):

$$\mathrm{Cov}(w_s, w_{s'}) = \sigma^2 \frac{1}{2^{\nu-1}\Gamma(\nu)}(\kappa\|s - s'\|)^\nu K_\nu(\kappa\|s - s'\|);$$

where: σ^2 is the marginal variance of the process; ν is the smoothness parameter (usually set to 1); κ is a scaling parameter (linked to the range ρ of the process by: $\rho = \sqrt{8\nu}/\kappa$); and K_ν is the modified Bessel function of the second kind. The range ρ of the process gives information on the spatial correlation range between points.

In the following, we distinguish between control variables (land use in the squares with the PCA axes and climate variables) which account for known confounders, and variables of interest describing the land sharing/sparing gradient.

Inference

We relied on a Bayesian framework for inference. Instead of using the traditional Monte Carlo Markov Chain algorithm to get posterior marginals, we used the Integrated Nested Laplace Approximation (`INLA`) developed by Rue et al. (2009). It provides fast and accurate deterministic approximations of posterior distributions for latent Gaussian models.

In particular, it computes posterior marginals for latent effects (regression coefficients) as well as for hyperparameters (variance of spatial and temporal random effects). This approach makes it possible to fit computationally demanding spatio-temporal models efficiently.

Prior choice As it is a Bayesian framework, we have to choose priors. They are summarized in Table 1. For the spatial field, we chose to use penalized complexity (PC) priors (Simpson et al. 2017) because it helps in choosing less complex models by penalizing the complexity of the latent Gaussian random field.

The spatial random field needs two parameters: the range, giving information about the spatial correlation range between two points and the variance of the distance of interaction σ (in the Matérn field). We chose to set the interaction range at 100 km because birds return to the same nesting sites (Jiguet et al. 2012; Fontaine et al. 2021; Barbet-Massin et al. 2012). For the variance we chose $\sigma = 1$ as a weakly informative prior.

All the other priors are default `INLA` priors that are weakly informative and are summarized in Table 1.

Mesh choice The first thing to do is to choose a mesh for the spatial random field. The mesh is automatically constructed by `INLA`, but we need to choose three parameters: the inner edge, the outer edge and the cutoff value. To avoid any boundary effects in the analysis, the mesh should be extended further away from the spatial domain (Lindgren et al. 2011). The inner edge sets the maximum length of an edge inside the spatial domain. In Dambly et al. (2023) they suggest to use inner edge as 1/5 the prior range, we assumed an interaction range of approximately 100 km, so we took 20 km. The outer edge sets the maximum length of an edge outside the spatial domain. In Righetto et al. (2020) they show that the outer range does not make so much difference and shall be bigger than the prior range, we chose 200 km. The cutoff value sets the minimal distance between two points in the mesh. As we

Table 1 Summary of prior distributions used in the INLA spatio-temporal models

Model component	Prior distribution	Interpretation / Notes
Spatial random field	PC on range and σ	$\Pr(\text{range} < 100\,000) = 0.99$, $\Pr(\sigma > 1) = 0.01$
SPDE smoothness	Fixed to $\alpha = 2$	Corresponds to a Matérn field with moderate smoothness ($\nu = 1$)
Temporal random effect	PC priors on ϕ and τ	Shrinks toward $\phi = 0$ (no auto-correlation) and small variance
Fixed effects	$\mathcal{N}(0, 10^6)$	Weakly informative / nearly flat prior
Negative binomial dispersion	$\log(\theta) \sim \mathrm{Gamma}(1, 0.00005)$	Weak prior on overdispersion parameter

PC stands for penalized complexity

cannot have observations that are less than 2 km away we chose the cut-off to be 2 km.

In Krainski et al. (2018) they mention that the mesh needs to be even in size and angle of the triangles of the mesh. It is the case with the values we chose (see Fig. SI-6).

Model selection

We have five groups of species of interest: woodland species, farmland species, generalist species, woodland species with conservation concern and farmland species with conservation concern (see Table SI-8 for the list of species of each group). We want to test the following set of variables: latitude, minimum temperature of previous spring and previous summer, maximum temperature of previous spring and previous summer, total amount of rain of previous spring, the first three variables from the PCA on the land cover of each square ($PC_{agri/forest}$, PC_{urban}, PC_{open} from Section "Correlation study and Principal Component Analysis (PCA) on the land cover variables" and see Table SI-1 for the loading of different land uses onto the PC axes), the Shannon index on agricultural practices (Section "Land sharing and sparing indicators"), total surface of forest in a radius of 10 kilometers around the center of the square and the surface of farmland with significant amount of nature in a radius of 10 kilometers around the center of the square. To these variables, we added interactions between on the one hand maximum temperatures (of last spring and summer) and on the other hand latitude, surface of forest 10 kilometers around, surface of agriculture with significant amount of nature 10 kilometers around and Shannon index. This yielded a total of 12 variables and 8 interactions to test.

Testing possible model combinations for each group of species would be computationally intensive (around 10 s per model with more than 4000 models by group). We thus chose to perform stepwise selection to find the covariates that explain best the data, following the approach in Illian et al. (2013). The criterion we used to select is the Widely Applicable Information Criterion (WAIC) as for example in Carson and Mills Flemming (2014). This criterion decreases when the fit of the model is better and penalizes the number of covariates. The WAIC gives a criterion of the goodness of fit of the model. However, it is a criterion that we can only use to compare models that are fitted to the exact same data and mesh parametrization (Dambly et al. 2023).

To test a wide range of models, we performed stepwise selection in three ways (Burnham and Anderson 2004): forward, backward and both. The forward procedure starts with the model with only random effects and then adds variables one by one. At each step, it selects the best variable to add to the model, according to the decrease of the WAIC score. When the two variables of an interaction are added, the corresponding interaction variable is added. Then, the backward procedure starts with the full model (all covariates and interaction) and remove one by one the covariates or interaction term along the same principle. Note that a covariate cannot be removed if an interaction term between this variable and another one is still in the formula. Finally, the "both" procedure starts as the forward procedure. After choosing a new variable to add, we add a backward step: we try to remove one by one each variable added in previous steps. We keep the model with the lowest WAIC after this backward step.

Results

We performed model selection for our five categories of birds. Detailed results can be found in Supplementary Table SI-2 for agricultural birds, Supplementary Table SI-3 for forest birds, Supplementary Table SI-4 for generalist birds, Supplementary Table SI-5 for agricultural birds with conservation concern and Supplementary Table SI-6 for forest birds with conservation concern.

First, we observed that in each category $PC_{agri/forest}$ has been chosen and is significant. Recall that this variable represents farmland squares when negative and forest squares when positive (Supplementary Fig. SI-7a and Table SI-1). Then, we observed that each variable has been selected for at least one category of species. Regarding interactions, three of them have never been chosen by the selection procedure: Shannon index with last spring maximum temperature, Shannon index with last summer maximum temperature, and latitude with last summer maximum temperature.

Then, Table 2 and 3 indicate that, for all groups of species, there is a strong temporal autocorrelation ($\phi \approx 0.9$) and that the range of the Matérn field is not bigger than 40 km, meaning that the probability that two points more than 40 km apart depend on each other is very low. We can also observe that the over-dispersion parameter is relatively high (from 11.64 to 47.25 Tables 2 and 3).

Fixed effects are shown in Fig. 2 for agricultural birds (A), forest birds (B) and generalist birds (C) and in Fig. 3 for agricultural (A) and forest (B) birds with conservation concern.

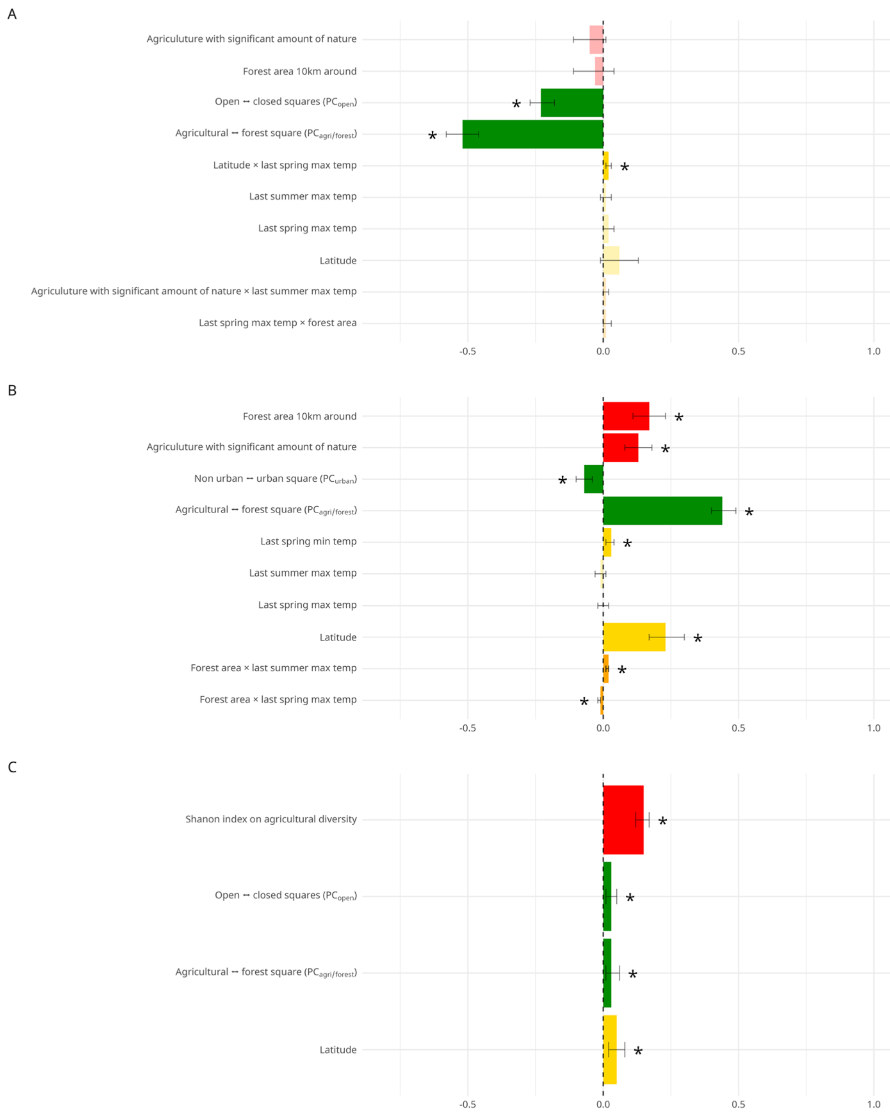

Fig. 2 Fixed effects of the best model for farmland species (**A**), woodland species (**B**) and generalist species (**B**). The variables highlighted in red are the land sharing and land sparing variables, the ones in green are about the land use of the squares, the ones in yellow represent climate variables and the orange ones are interactions between land sharing and sparing variables and climate. Significant variables are represented in plain color and with a star whereas non-significant variables are transparent

Table 2 Mean values of the posterior distribution of hyperparameters

Model component		Agricultural birds	Forest birds	Generalist birds
Spatial Random field	ρ (m)	17435.26	18336.21	13071.93
	σ	0.79	0.72	0.39
Temporal model	ϕ	0.89	0.60	0.89
	τ	111.48	367.41	359.25
Negative binomial dispersion		11.64	47.25	42.30

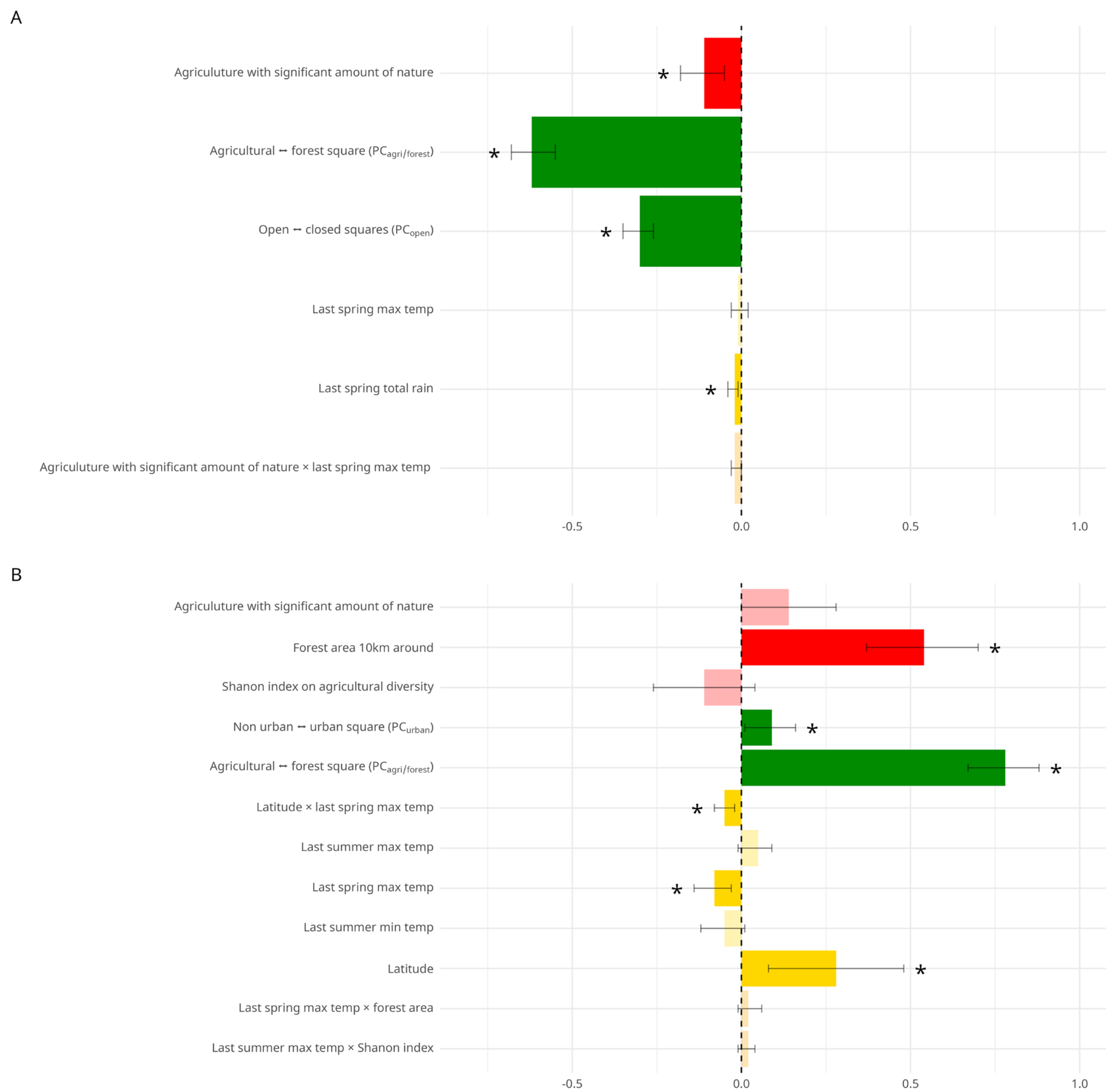

Fig. 3 Fixed effects of the best model for farmland species with conservation concern (**A**) and woodland species with conservation concern (**B**). The variables highlighted in red are the land sharing and land sparing variables, the ones in green are about the land use of the squares, the ones in yellow represent climate variables and the orange ones are interactions between land sharing and sparing variables and climate. Significant variables are represented in plain color and with a star whereas non-significant variables are transparent

Table 3 Mean values of the posterior distribution of hyperparameters for birds with conservation concern

Model component		Agricultural birds	Forest birds
Spatial Random field	ρ (m)	18480.75	36334.33
	σ	1.01	1.46
Temporal model	ϕ	0.92	0.92
	τ	129.18	24.74
Negative binomial dispersion		29.51	12.87

The models use two kinds of control variables (land use and climate). Firstly, the land uses are described by the three first PCA axes: $PC_{agri/forest}$ (negative for agricultural squares and positive for forest squares), PC_{urban} (positive for urban square) and PC_{open} (negative for open squares and positive for closed squares) (see Section "Correlation study and Principal Component Analysis (PCA) on the land cover variables" and y material Section "Materials and Methods"). $PC_{agri/forest}$ is significant (when the confidence interval does not include zero) for all group of birds, positive for forest birds (**0.44**, with Credible Interval [0.40, 0.49]), forest birds with conservation concern (**0.78** [0.67, 0.88]) and generalist birds (0.03 [0.01, 0.06]), and negative for farmland birds (**− 0.52** [−0.58, −0.46]) and farmland birds with conservation concern (**− 0.62** [−0.68, −0.55]). PC_{urban} is selected and significant for forest birds (**− 0.07** [−0.10, −0.04]) and forest birds with conservation concern (**0.08** [0.01, 0.16]). PC_{open} is selected and significant for agricultural birds (**− 0.23** [−0.27, −0.18]) agricultural birds with conservation concern (**− 0.30** [−0.35, −0.26]) and generalist birds (**0.03** [0.01, 0.05]).

Then the other set of control variables was composed of climate variables and latitude. Last spring minimum temperature was selected and significant for forest birds (**0.03** [0.01,0.04]). Last spring maximum temperature was selected and significant for forest birds with conservation concern (**−0.08** [− 0.14,− 0.03]). It was also selected but not significant for forest birds, agricultural birds and agricultural birds with conservation concern. Last spring total amount of rain was selected and significant for agricultural birds with conservation concern (**− 0.02** [− 0.04,− 0.01]). Last summer minimum temperature was selected but not significant for forest birds with conservation concern. Last summer maximum temperature was selected but not significant for agricultural birds, forest birds, and forest birds with conservation concern. The interaction between last spring maximum temperature and latitude was selected and significant for forest birds with conservation concern (**− 0.05** [− 0.08,− 0.02]). Although some climate variables were selected and significant for some models, we observe that these have limited effects because of the very small coefficients. However, when climate variables were selected and significant, results are globally in line with those of Thepault et al. (2025).

In our approach the land sharing and sparing gradient is described thanks to three variables: agriculture with significant amount of nature, Shannon index and forest area in a radius of 10 km around.

For agricultural birds (Fig. 2A) agriculture with a significant amount of nature and forest area 10 kilometers around were selected but not significant (respectively − 0.05 [− 0.11,0.01] and − 0.03 [− 0.11,0.04]). Some interaction between these variables and climate variables were also selected but not significant.

For forest birds (Fig. 2B), two variables of interest were selected and significant: forest area and agriculture with a significant amount of nature 10 kilometers around (respectively **0.17** [0.11,0.23] and **0.13** [0.08, 0.18]). Interactions between overall forest area and last spring and last summer maximum temperature were selected and significant (respectively **− 0.1** [− 0.02, − 0.01] and **0.01** [0.01, 0.02]).

For generalist birds (Fig. 2C) the Shannon index on agricultural diversity was selected and significant (**0.15** [0.12,0.17]).

These results on all species primarily indicate that a land sparing scenario is better for forest and agricultural species and a land sharing scenario is better for generalist species.

We next examined the responses of species of conservation concern (Fig. 3). For agriculture birds with conservation concern (Fig. 3A), the only land sharing/sparing variable selected was agriculture with a significant amount of nature and is significant (**− 0.11** [− 0.18,− 0.05]). For forest birds with conservation concern all three variables have been selected but only the area of forest 10 kilometers around was significant (**0.5** [0.37,0.70]). These results on birds with conservation concern showed that land sharing is not the preferred solution in order to conserve these species.

Discussion

In this study, we aimed to disentangle the impacts of land sharing and land sparing on French bird populations. Note that in a land sparing scenario, the goal is to divide landscape into a zone of high production agriculture and an area dedicated to biodiversity conservation whereas in a land sharing scenario, the landscape is shared between areas of food production and biodiversity conservation (with for example natural structures inside farmland areas).

First, as expected, the land use PCA axes confirmed that each group of birds is more abundant in its preferred habitat: farmland species in agricultural squares, forest species in forested squares. It is consistent with the concept of habitat specialization (Devictor et al. 2010). The spatial range of the Matérn field (below 40 km) is also consistent with known bird breeding ecology, as natal dispersal distances are typically around 14 km (Barbet-Massin et al. 2012), further supporting the validity of our spatial model. Then, our results showed that in the French bird community there is a diversity of response to the land sharing and land sparing gradient depending on habitat specialization (farmland, woodland, generalist) and conservation concern. Hence, land sharing seems to be beneficial for generalist species, as the abundance of this group increases if there is more diversity in agricultural practices. This result aligns with the main hypothesis because a land sharing scenario includes small and many kinds of habitats that offer a wide variety of nesting sites and resources that benefit species that do not have strict requirements in terms of resources such as habitat or food (Martin and Fahrig 2018). At the scale of our study (a 10 km buffer around 810 sites across France) land sparing seems to be the best scenario for all other species group with no conservation status. Indeed, for forest species our results showed that land sparing scenario is better, because the abundance of this group increases with a greater forest area, which aligns with our hypothesis. The variable "agriculture with a significant amount of nature" was also selected with a positive coefficient. This result can be explained by the study by Monnet et al. (2026) that showed pesticides impact all birds and the fewer constraint forest species face, the better they perform. Regarding farmland species, unexpectedly, our results showed that a land sparing scenario is also preferable. This may be explained by the fact that in Europe we are already mostly in a land sharing scenario (Karner et al. 2019) and that being in a more heterogeneous landscape would imply a habitat that is not the one they are specialized in.

Our results showed that the land sparing scenario is better for forest species with conservation concern because the abundance increases with a greater forest area.

For agricultural species with conservation concern it may appear counterintuitive that their highest abundances are observed in land sparing scenarios, i.e., areas with a low proportion of natural habitats such as bushes and hedges. This pattern might suggest that farmland birds of conservation concern do not benefit from these semi-natural elements. However, this interpretation is likely misleading. We argue that ground-nesting farmland bird species, which are now the primary focus of conservation efforts, have become particularly vulnerable in intensive agricultural landscapes. This vulnerability stems from decades of agricultural mechanization and intensification. Our analysis of land use within survey squares further supports this hypothesis because birds with conservation concern are more abundant in farmland and open landscapes. Hence, as shown in recent literature (Monnet et al. 2026; Rigal et al. 2023), farmland birds are declining because of the intensification of agricultural practices and pesticide use. We note that our group of farmland birds of conservation concern encompasses species with contrasting habitat requirements: ground-nesting open-landscape specialists but also shrub-dependent species. Future work with larger datasets could benefit from analyzing these subgroups separately.

In order to answer the question of how to allocate land use to conserve biodiversity our results showed that there is not one agricultural practice to prefer to conserve all groups of birds. Indeed, land sharing is better for generalist species whereas land sparing is better for forest and agricultural species. However, as shown in Rigal et al. (2023) farmland birds are declining; therefore, even if land sharing is not the primary solution, we still consider a more biodiversity friendly agriculture to conserve bird populations. As shown in Monnet et al. (2026) pesticides are one of the drivers of this decline, so reducing their use could therefore be a key solution. Overall, we cannot conclude that farmland birds with conservation concern prefer land sparing. Despite their apparent specialization in intensive agricultural landscapes, our findings suggest that conserving these species should prioritize reducing chemical inputs and adopting wildlife-friendly practices within larger field structures, rather than intensifying management further.

A main limitation of our analyses is the long time series of the STOC database. Indeed, over this timescale the only available land use database is the

CLC database. The resolution of this database might be too low to capture changes in bird abundance as mentioned in Gottschalk et al. (2011). Similarly, forest quality variables such as vertical stratification, tree age, or deadwood proportion were not available at the scale of this study. Although CORINE land cover distinguishes between broadleaved, coniferous and mixed forests, we aggregated all forest types into a single forest area variable. As our main focus is on farmland birds, and given that the species–area relationship supports a predictable increase in abundance with forest area (Arrhenius 1921; Preston 1962), this approximation remains suitable to address our central question on land allocation Moreover, there are no data on pesticides use, as the ones used in Monnet et al. (2026) only start in 2015 and the ones used in Perrot et al. (2025) start in 2008. There are also no data available on small natural structures inside (hedgerow monitoring started in 2022 (Preux 2025)) fields. The indicators we used are thus, the most appropriate variables available for this study period to account for land use heterogeneity (with the Shannon index on agriculture practices), the presence of natural structures in fields (agriculture with a significant amount of nature), as well as big conserved forest. These three variables summarize well different characteristics Then, we did not take into account detection bias, but we aggregated observations at the survey-square scale to reduce randomness of detectability bias (Nabias et al. 2024).

In conclusion, our findings underscore a widespread challenge in agricultural landscapes akin to those in France: striking a balance between biodiversity conservation and agricultural production, particularly for species of conservation concern that depend on habitats shaped by intensive farming.

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Author contributions All authors contributed to the study conception and design. Material preparation and (online) data collection was performed by A.E. Data analysis was performed by A.E. and R.L. The first draft of the manuscript was written by A.E. and all authors commented on previous versions of the manuscript. A.E. made the revisions needed after the reviewers reports. All authors read and approved the final manuscript.

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Data availability The bird abundance data analyzed during the current study are available on reasonable request on Vigie-Nature website (https://www.vigienature.fr/fr/acceder-aux-donnees). Climate data are available on WordClim website (https://worldclim.org/data/monthlywth.html). Land use data are available on Copernicus Website (https://land.copernicus.eu/en/products/corine-land-cover).

Code availability `R` code used for analysis is available at https://github.com/adelieerard/birds_inla.

Declarations

Conflict of interest The authors declare no conflict of interest.

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