Disentangling land sharing and land sparing effects on bird abundance in France using spatio-temporal Bayesian modeling

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February 19, 2026

Abstract

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. Two contrasting strategies are commonly discussed: land sparing, characterized by intensive agriculture combined with large, separate natural areas, and land sharing, where low-intensity agriculture is embedded within heterogeneous, wildlife-friendly landscapes. However, empirical evidence remains mixed, and few studies have quantified these strategies along a continuous gradient while accounting for spatial and temporal ecological processes.

Using data from the French Breeding Bird Survey (STOC-EPS), we analyzed bird abundance in 810 locations monitored between 2001 and 2024. We quantified a land sharing–sparing gradient using (i) forest area within a 10 km radius, (ii) agricultural land with significant amount of nature, and (iii) a Shannon diversity index of agricultural patches. Bird counts were modeled with negative binomial spatio-temporal Bayesian models fitted using the Integrated Nested Laplace Approximation (INLA), incorporating climate variables, land cover structure, spatial random fields, temporal autocorrelation, and interaction terms. Model selection was performed using WAIC across five species groups: farmland, forest, generalist, and species of conservation concern within farmland and forest habitats.

We found contrasting responses among ecological groups. Forest birds, including species of conservation concern, were positively associated with greater forest area, supporting a land sparing strategy. Generalist species responded positively to higher agricultural heterogeneity, consistent with land sharing benefits. Contrary to expectations, farmland specialists did not benefit from increased agricultural heterogeneity, and farmland species of conservation concern were negatively associated with farmland containing substantial natural elements. Across groups, strong spatial and temporal autocorrelation highlighted the importance of explicitly modeling ecological structure.

Our results demonstrate that no single land-use strategy maximizes abundance across all bird groups. Land sparing appears more favorable for forest specialists and conservation-priority species, whereas land sharing

benefits generalists. These findings underscore the need for context-dependent landscape planning and suggest that biodiversity-friendly agricultural practices must be tailored to species ecological requirements rather than relying on a single land management paradigm.

1 Introduction

With the current global biodiversity decline [Burns et al., 2021, Inger et al., 2015], land use allocation is a major challenge to conserve biodiversity. Agricultural landscapes are central to this issue, as they cover a large proportion of European territory and host a substantial share of biodiversity. Several studies show that farmland birds are declining in Europe [Donald et al., 2001, Bowler et al., 2019]. This decline is mainly explained by the intensification of farmland practices [Rigal et al., 2023, Genty et al., 2026] and pesticide use [Monnet et al., 2026, Perrot et al., 2025]. [Heldbjerg et al., 2018] authors also show that birds that nest on the ground are in significant decline in Denmark whereas birds nesting elsewhere are less impacted. This leads to the question of: how land should we divided to maximize biodiversity? Two main schemes of practices are known today [Fischer et al., 2014, Grass et al., 2019, Fahrig, 2020, Fahrig, 2013]:

- Land sparing where the agricultural production in highly intensive farmland and conservation areas are separated to minimize trade-offs between food production and biodiversity preservation. Hence, in these landscapes' structuration there are often a very low diversity in agricultural area caraterised by homogeneous patches, and high intensity farmland practices and high biodiversity in some big protected area as national reserves and forest.

- In the other hand the land sharing aims to support both food security and biodiversity by the coexistence of agriculture and biodiversity conservation in the same place. This kind of landscape is often characterized by a lot of small patches of fields with trees and hedges between them. In this case, the landscape is heterogeneous and there is a high connectivity between patches and farmland practices are usually low intensity.

However, we are never in the full scenario of land sparing nor land sharing, and we should rather consider a spectrum between them[Fahrig, 2013].

Indeed, on the one hand [Phalan et al., 2011, 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 more 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] offers a solution with three compartments enabling some big forests to conserve woodland birds, some low intensity agriculture to conserve farmland birds and some big fields to ensure food security. In these studies, there is no consensus on how to construct an indicator of land sharing and land sparing other than the fact that it is linked to food production.

More than half of France is covered by farmland [European Environment Agency, 2019] with a high diversity in practices [Nagy and Soós, 2025].

Monitoring of bird species abundance to document the effects of human activities on biodiversity has received much attention in the ecological literature, particularly because birds are easy to sample, they cover a wide life history trait, they are present in all habitats and trophic levels [Padoa-Schioppa et al., 2006, Karen Aghababyan, 2024], and they are sensitive to environmental stressors [Canterbury et al., 2000, Gregory et al., 2003, Rigal et al., 2023].

Moreover, citizen science allow an easy data collection for birds because a lot of volunteers are skilled to recognized birds. Hence, thanks to thousands of French skilled bird watcher we gathered and impressive database of a long term survey of breeding bird (French Breeding Bird Surveys - FBBS) [Jiguet et al., 2012, Fontaine et al., 2021].

As indicators of land sharing and sparing are complex, we need to take into account a lot of variables that structure the landscape and bird populations. Moreover, to take into account the spatio-temporal framework, a Bayesian framework seems to be the most suitable.

In this study, we use spatio-temporal Bayesian modeling to show the effects of land sharing and sparing scenario on bird populations. 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.

2 Materials and Methods

2.1 Data

2.1.1 Bird abundance data

The data are provided by the French Breeding Bird Survey [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. 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 minutes at each point and recording every seen or heard bird [Jiguet et al., 2012].

In order to have clean data, we removed every square that has not been observed in the right times and dates. We also removed squares that do not have ten points in it (around 2% of the data). Then we chose to aggregate data to the scale of the square (sum of all points) to feasibly carry out statistical analysis made by `INLA` and remove detectability bias [Nabias et al., 2024].

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 point 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 STOC 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 and Kirwan, 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]. Then, we used the French UICN list [UICN France et al., 2016] to classify the species in two categories: least concerned and birds with conservation concern. In the French UICN list [UICN 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.

2.1.2 Environmental data

Climate data is taken from WordClim [Harris et al., 2020]. For each square and year we retrieved minimum and maximum temperatures and total amount of precipitation of the current and last spring (March to June) as well as minimum and maximum of last summer (July and August). Then we added the latitude, recentered to be positive when in the North and negative otherwise. This variable also serves through interactions with the location and climate variables, allowing us to check if our model works well by finding the same results as in [Thepault et al., 2025].

We used CORINE land cover [European Environment Agency, 2019] to retrieve land cover variables. This database contains all land uses in France in a raster format for years 2000, 2006, 2012 and 2018. The different kind of land uses are described in 44 groups (4). For each year, we retrieved in each square the surface of agricultural (all CORINE codes starting by 2) and water areas (all CORINE codes starting by 5), forest (all CORINE codes starting by 31), natural (all CORINE codes starting by 32 or 33), water (all CORINE codes starting by 4 or 5) and artificial lands (all CORINE codes starting by 1). This gives us a general idea of the use of each square. We did a linear interpolation of the data when it was not constant between two years of data.

2.1.3 Land sharing and sparing indicators

To create indicator of land sharing and land sparing we took the intersection of CORINE patches and a disk of radius $10km$ centered in the middle of each square. It gave us, 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).

In order 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 patch and the abundance the number of each kind of patch. Shannon's indices will give us an idea of the diversity of agricultural land uses around each square. If this index is high then there is a big 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 Figure 1.

The last two variables we added are the amount of forest and agriculture with significant amount of nature in a radius of 10 kilometers around the point of interest. A higher amount of forest implies a land sparing scenario whereas a higher amount of agriculture with significant amount of nature implies a land sharing scenario.

2.1.4 Correlation study and Principal Component Analysis on the land cover variables

The land use of each square consists of six highly correlated variables as they all sum up to the area of the square (4 square kilometers). We then use a PCA to summarize these variables onto fewer variables that are not correlated. After computations, we can summarize into three component explaining 80.8% of the variance of the data (Figure 2c). The axes are represented in Figures 2a and 2b. The first axis separates the agricultural squares (negative) from the natural and forest squares (positive). The second axis separates urban (and water) squares (positive) with the others. The third axis separates closed squares (forest and cities) from the open squares (flat lands). We call these axes PCA1, PCA2 and PCA3.

2.2 Statistical approach

2.2.1 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

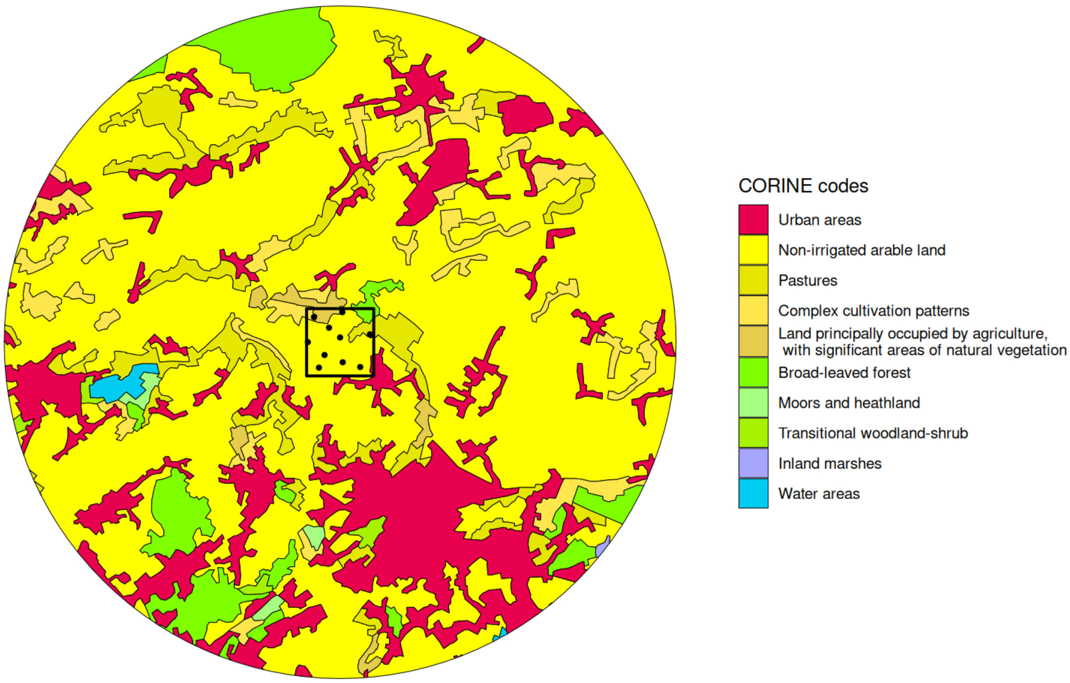
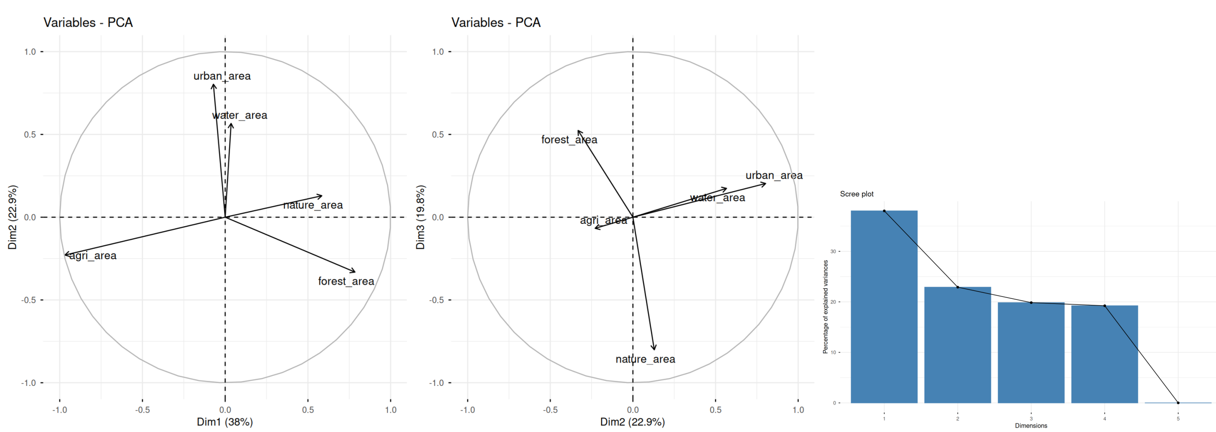


Figure 1: Example of the land use in a 10 km radius disk around a square (black line). Each color represents a different kind of land use following the table in Appendix 4. Shannon's indices are calculated only with agricultural patches (codes starting with a two). In this case there are 68 agricultural patches spread in four categories. The black dots represent ten points of samples.



(a) Axis 1 and 2 (b) Axis 2 and 3 (c) Eigenvalues

Figure 2: Results of the PCA on the land cover of each square

regression model, which accounts for overdispersion in the data due to the lack of observation as well as for real bird distribution. Formally, the expected abundance at location s and year t is defined as:

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

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:

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

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:

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

where ϕ is the auto-correlation parameter and τ is the precision parameter. For the spatial Matérn random field, the covariance is as following (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 maximum distance of interaction between points.

2.2.2 Inference

We relied on a Bayesian framework for inference. Instead of using the traditional MCMC algorithm to get posterior marginals, we used the Integrated Nested Laplace Approximation [Rue et al., 2017] (`INLA`). 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 some priors. They are summarized in Table 1.

Table 1: Summary of prior distributions used in the INLA spatio-temporal models. PC stands for Penalized Complexity

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	$\log(\theta) \sim \text{Gamma}(1, 0.00005)$	Weak prior on overdispersion parameter

For the spatial field, we chose to use penalized complexity (PC) priors [Simpson et al., 2017] because it helps in choosing less complex model by penalizing the complexity of the latent Gaussian random field.

The spatial random field needs two parameters: the range, giving information of the maximum distance of interaction between two points and the variance of the distance of interaction σ (in the Matérn field). We chose to set the range of interaction at 100 km because birds will come back to the same place to nest [Jiguet et al., 2012, Fontaine et al., 2021]. 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 suppose the range of interaction to be around 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 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 Figure SI-6).

2.2.3 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. We want to test the following set of variables: latitude, minimum temperature of last spring and last summer, maximum temperature of last spring and last summer, total amount of rain of last spring, the first three variables from the PCA on the land cover of each square (PCA1, PCA2, PCA3 from Section 2.1.4), the Shannon index on agricultural practices (Section 2.1.3), 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 brings us to a total of 12 variables and 8 interactions to test.

Testing all models for each group of species would take a lot of time (around 10 seconds 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, as 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 can not 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.

3 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-4 for forest birds, Supplementary Table SI-5 for generalist birds, Supplementary Table SI-1 for agricultural birds with conservation concern and Supplementary Table SI-3 for forest birds with conservation concern.

First, we observed that in each category PCA1 has been chosen and is significant. Recall that this variable represents farmland squares when negative and forest squares when positive (Figure 2a). Then all variables have been chosen at least in one group of birds. 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, we can see in Table 2 and 3 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 that are more than 40 km depend on each other is very low. This distance aligns with the knowledge about bird breeding ecology as the breeding site fidelity and the distance of natal dispersal is known to be around 14 km (with 16 km of standard deviation) [Barbet-Massin et al., 2012]. We can also observe that the overdispersion parameter is pretty high (from 11.64 to 47.25 Table 2 and 3).

Fixed effects are shown in Figure 3 for agricultural birds (A), forest birds (B) and generalist birds (C) and in Figure 4 for agricultural (A) and forest (B) birds with conservation concern.

The models use two kinds of **control variables** (land use and climate). Firstly, the **land uses** are described by the three first PCA axes: PCA1 (negative for agricultural squares and positive for forest squares), PCA2 (positive for urban square) and PCA3 (negative for open squares and positive for closed squares) (see 2.1.4). PCA1 is significant (when the confidence interval does not include zero) for all group of birds, positive for forest birds (**0.44**, with Confidence 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**, $[-0.68, -0.55]$). PCA2 is selected and significant for forest birds (-0.07, $[-0.10, -0.04]$) and forest birds with conservation concern (0.08, $[0.01, 0.16]$). PCA3 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, $[0.01, 0.05]$). These results are in line with the usual hypotheses that the abundance of a group of birds increases in the habitat they are specialized in.

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, CI [-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 do not have so much effect 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 kilometers around.

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

Table 2: Mean values of the posterior distribution of hyperparameters

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

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

For agricultural birds (Figure 3-A) 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 (Figure 3-B), 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 (Figure 3-C) the Shannon index on agricultural diversity was selected and significant (0.15, [0.12,0.17]).

These results on all species mainly show 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 (Figure 4). For agriculture birds with conservation concern (Figure 4-A), 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 solution to prefer in order to conserve these species.

4 Discussion

Our results first showed that for generalist birds a land sharing scenario is better because the abundance increases if there is more diversity in agricultural practices. This is in line with our main hypothesis because a land sharing

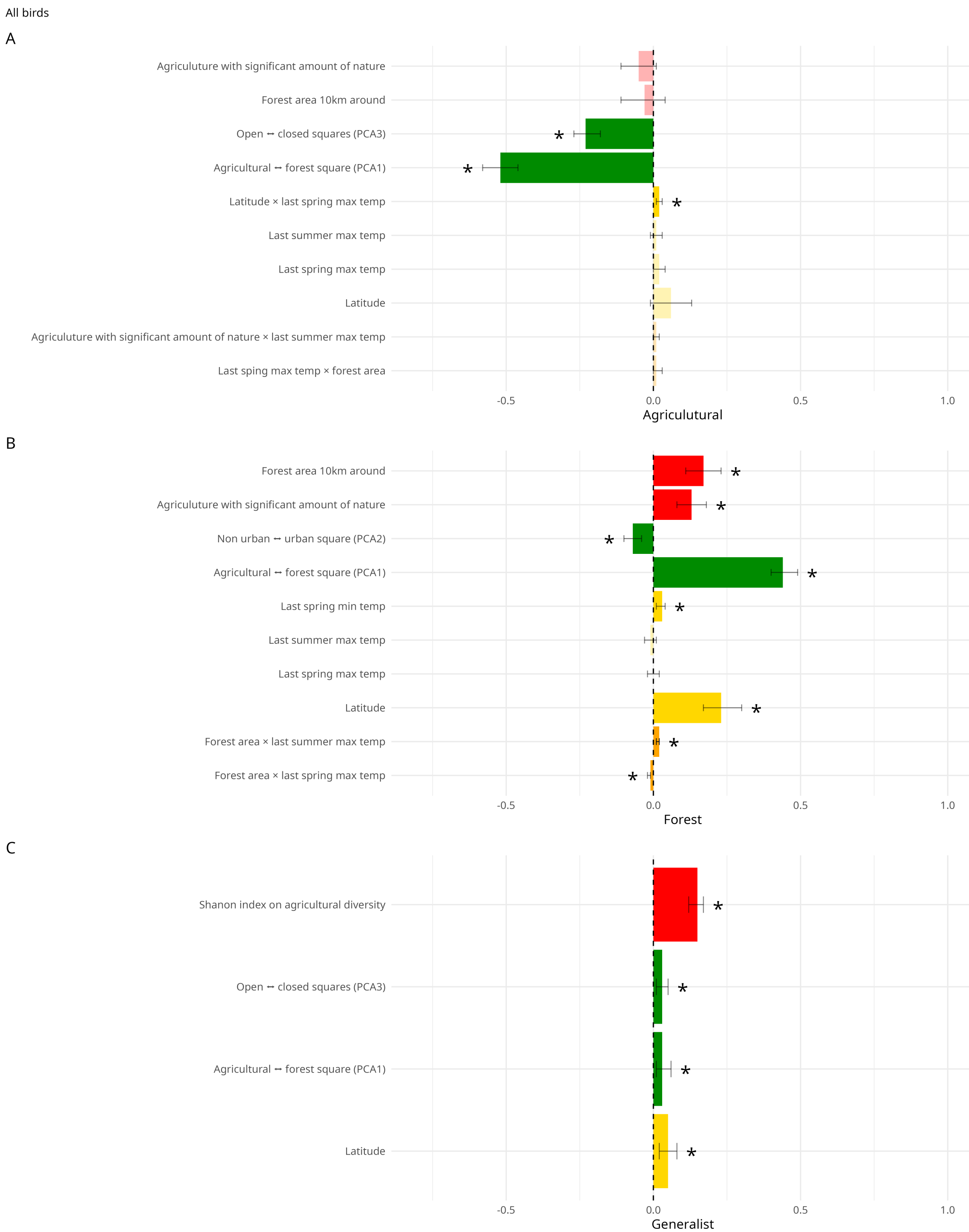


Figure 3: Fixed effects of the best model for farmland species (A), woodland species (B) and generalist species (C). The variables highlighted in red are the land sharing and land sparing variables, the ones in green are about the land use of the squares, the one in yellow represent climate variables and the orange one 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.

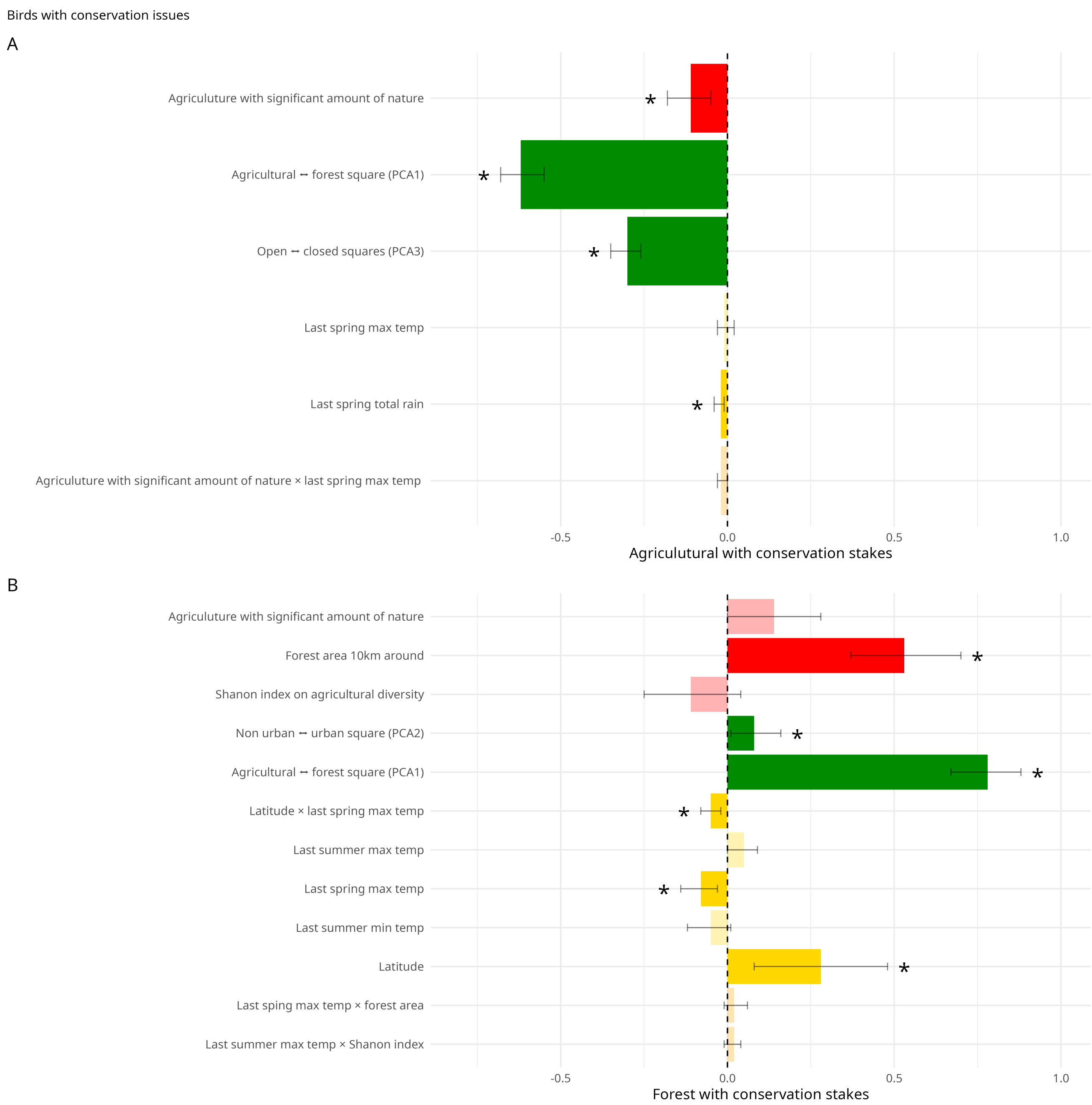


Figure 4: Fixed effects of the best model for farmland species with conservation concern (A) and woodland species with conservation concern(B). The variables highlighted in red are the land sharing and land sparing variables, the ones in green are about the land use of the squares, the one in yellow represent climate variables and the orange one 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.

scenario includes more small habitat to nest. However, our results do not showed that a land sharing scenario is better for agricultural birds. This was unexpected and may be explained by the fact that in Europe we are already mostly in a land sharing scenario and that being further on the land sharing spectrum would imply a habitat that is not the one they are specialized in. For forest birds, our results showed that the land sparing scenario is better. This is in line with our hypothesis.

The variable agriculture with significant amount of nature was selected only for forest birds. We thought that it would only be favorable to agricultural species, but it was selected and significant with a positive coefficient for forest birds. This might be because, as shown in [Monnet et al., 2026], pesticides impact all birds and the less constraint forest species get the better they are.

Regarding species with conservation concern, we found that the land sparing scenario is better for forest species. For agricultural species with conservation concern, we showed that farmland with a high amount of nature is not the preferred scenario. This can be explained by the fact that agricultural birds with conservation concern nest on the ground and thus do not benefit from bushes and hedges. Coupled with the results on the land use of the squares, our results suggested that to conserve agricultural birds with conservation concern we should have more farmland or open land. However, as shown in [Monnet et al., 2026], farmland birds are declining because of pesticide use. The scenario to prefer should then be a land sparing scenario with big open field but with a low yield agriculture.

Finally, we showed that the range of interaction of the spatial field is usually around 20 km. There is a first exception for forest birds with conservation concern for which the range of interaction is around 36 km. This can be explained by the lack of detectability of birds in forest areas [Nabias et al., 2024]. The other exception is for generalist birds that have a lower range of interaction (around 13 km) which can be explained by the fact that they do not have a preferred habitat and thus do not have to move that far away.

We can conclude 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 in decline so even if land sharing is not the solution we should maybe think about 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 it might be a solution to reduce their use.

Actually, we cannot say that farmland birds with conservation concern prefer land sparing. However, they are specialized in intensive agricultural landscapes. This is a limitation of our land sharing and sparing indicator and is due to the fact that the STOC database is a long time series (from 2001 to 2025). Indeed, pesticides data used in [Monnet et al., 2026] only start in 2015, the ones used in [Perrot et al., 2025] start in 2008. Both of them do not cover our time series, thus it is not applicable to our methods. To conclude on the indicators, the Shannon index on agricultural patches, the area of forest and agriculture with significant amount of nature in a radius of 10 kilometers are the most appropriate variables available for the study period.

Finally, one extension of this work could be to work on land sharing and sparing on all types of habitat (for example with urban habitat as in [Simensen, 2025]). It would allow us to discuss having biodiversity friendly land uses everywhere and especially in big cities where there is no space for biodiversity. Another extension would be to add a food production variable. Indeed, land sharing and sparing strategies are usually focused both on biodiversity conservation and agricultural yield. A challenge is actually to find the balance between biodiversity conservation and food security and a way of doing it would be to reduce livestock to have more space for biodiversity friendly agriculture and still enough resources to feed everyone.

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Supplementary material

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February 17, 2026

1 Maps

2 Tables of the results

	mean	sd	0.025quant	0.5quant	0.975quant	mode	kld
(Intercept)	1.10	0.05	1.00	1.10	1.20	1.10	0.00
Land3	-0.30	0.02	-0.35	-0.30	-0.26	-0.30	0.00
preci_last_spring	-0.02	0.01	-0.04	-0.02	-0.01	-0.02	0.00
surface_243_10km	-0.11	0.03	-0.18	-0.11	-0.05	-0.11	0.00
tmax_last_spring	-0.01	0.01	-0.03	-0.01	0.02	-0.01	0.00
Land1	-0.62	0.03	-0.68	-0.62	-0.55	-0.62	0.00
surface_243_10km:tmax_last_spring	-0.02	0.01	-0.03	-0.02	-0.00	-0.02	0.00

	mean	sd	0.025quant	0.5quant	0.975quant	mode
(1/overdispersion)	29.51	1.37	26.92	29.47	32.31	29.38
Range for spatial (m)	18480.75	1459.90	15740.59	18434.65	21484.56	18366.57
Stdev for spatial	1.01	0.03	0.95	1.01	1.07	1.01
Precision for annee_factor	129.18	76.50	25.76	113.24	312.73	74.57
Rho for annee_factor	0.92	0.05	0.80	0.93	0.99	0.96

Table SI-1: C birds agri

3 List of species with their habitat and conservation status

Table SI-6: Bird species by taxonomic order, habitat type and conservation status

Order	Species	Habitat type	Status
Accipitriformes	Buteo buteo	Agricultural	Least concerned
Passeriformes	Emberiza cirlus	Agricultural	Least concerned
Falconiformes	Falco tinnunculus	Agricultural	Conservation stake
Passeriformes	Lanius collurio	Agricultural	Conservation stake

Order	Species	Habitat type	Status
Passeriformes	Emberiza citrinella	Agricultural	Conservation stake
Passeriformes	Corvus frugilegus	Agricultural	Least concerned
Passeriformes	Sylvia communis	Agricultural	Conservation stake
Charadriiformes	Vanellus vanellus	Agricultural	Conservation stake
Galliformes	Coturnix coturnix	Agricultural	Least concerned
Galliformes	Alectoris rufa	Agricultural	Least concerned
Upupiformes	Upupa epops	Agricultural	Least concerned
Passeriformes	Saxicola rubicola	Agricultural	Conservation stake
Passeriformes	Passer montanus	Agricultural	Conservation stake
Charadriiformes	Burhinus oedicnemus	Agricultural	Conservation stake
Passeriformes	Lullula arborea	Agricultural	Least concerned
Passeriformes	Alauda arvensis	Agricultural	Conservation stake
Passeriformes	Emberiza calandra	Agricultural	Conservation stake
Passeriformes	Carduelis cannabina	Agricultural	Least concerned
Galliformes	Perdix perdix	Agricultural	Least concerned
Passeriformes	Motacilla flava	Agricultural	Least concerned
Passeriformes	Anthus pratensis	Agricultural	Conservation stake
Passeriformes	Phylloscopus collybita	Forest	Least concerned
Passeriformes	Turdus philomelos	Forest	Least concerned
Piciformes	Dendrocopos major	Forest	Least concerned
Passeriformes	Erithacus rubecula	Forest	Least concerned
Passeriformes	Regulus ignicapilla	Forest	Least concerned
Passeriformes	Troglodytes troglodytes	Forest	Least concerned
Passeriformes	Certhia familiaris	Forest	Least concerned
Passeriformes	Regulus regulus	Forest	Conservation stake
Passeriformes	Sitta europaea	Forest	Least concerned
Passeriformes	Lophophanes cristatus	Forest	Least concerned
Passeriformes	Phylloscopus bonelli	Forest	Least concerned
Passeriformes	Poecile palustris	Forest	Least concerned
Passeriformes	Certhia brachydactyla	Forest	Least concerned
Passeriformes	Turdus viscivorus	Forest	Least concerned

Order	Species	Habitat type	Status
Passeriformes	Phylloscopus sibilatrix	Forest	Conservation stake
Passeriformes	Phylloscopus trochilus	Forest	Conservation stake
Passeriformes	Pyrrhula pyrrhula	Forest	Conservation stake
Passeriformes	Coccothraustes coccothraustes	Forest	Least concerned
Piciformes	Dendrocopos medius	Forest	Least concerned
Passeriformes	Parus montanus	Forest	Least concerned
Passeriformes	Sylvia melanocephala	Forest	Conservation stake
Columbiformes	Columba palumbus	Generalist	Least concerned
Passeriformes	Corvus corone	Generalist	Least concerned
Passeriformes	Cyanistes caeruleus	Generalist	Least concerned
Passeriformes	Sylvia atricapilla	Generalist	Least concerned
Passeriformes	Turdus merula	Generalist	Least concerned
Passeriformes	Fringilla coelebs	Generalist	Least concerned
Passeriformes	Hippolais polyglotta	Generalist	Least concerned
Passeriformes	Parus major	Generalist	Least concerned
Passeriformes	Garrulus glandarius	Generalist	Least concerned
Cuculiformes	Cuculus canorus	Generalist	Least concerned
Passeriformes	Oriolus oriolus	Generalist	Least concerned
Piciformes	Picus viridis	Generalist	Least concerned
Passeriformes	Luscinia megarhynchos	Generalist	Least concerned
Passeriformes	Prunella modularis	Generalist	Least concerned

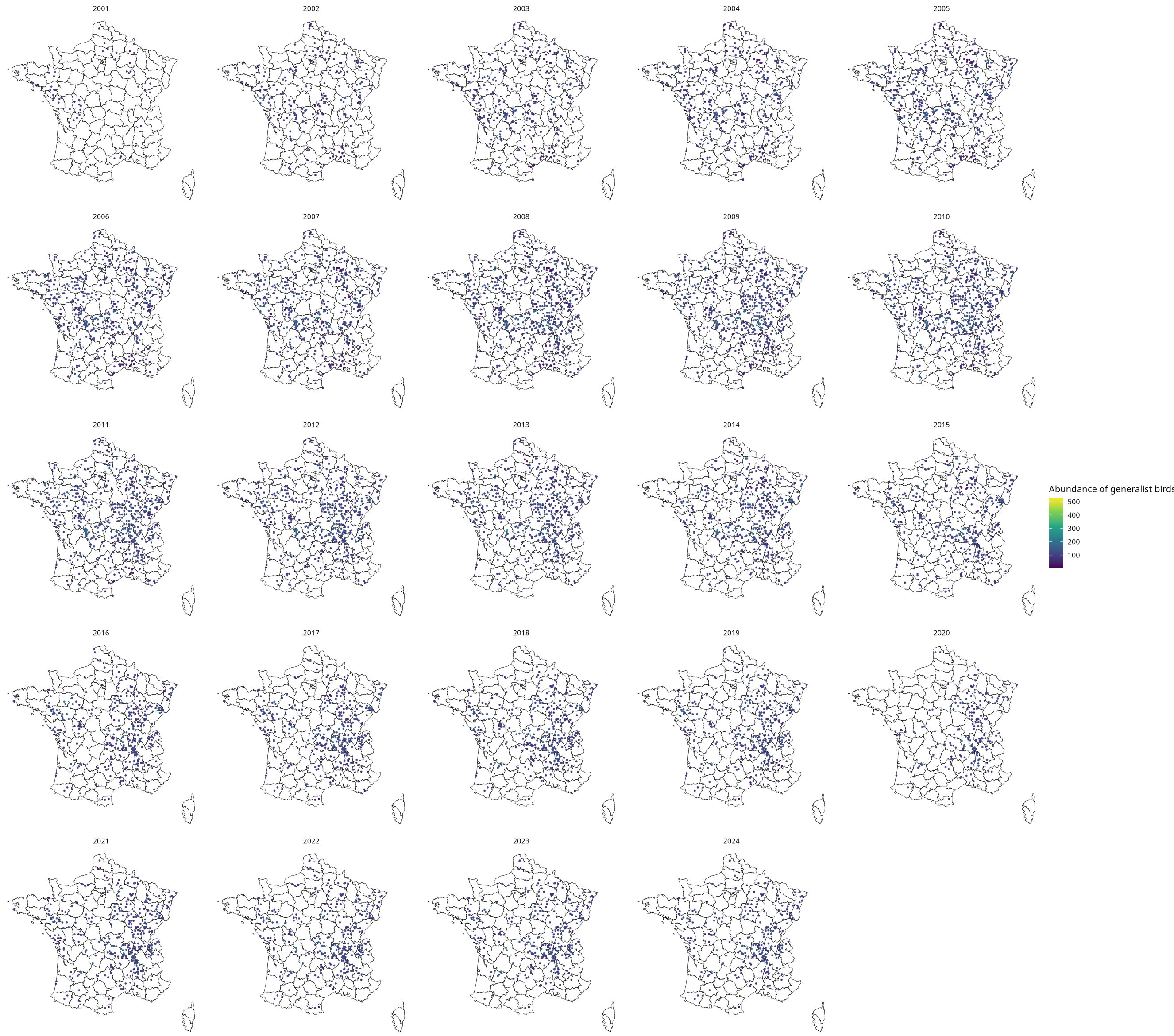

Figure SI-1: Abundance of generalist birds observed in the STOC program, by year

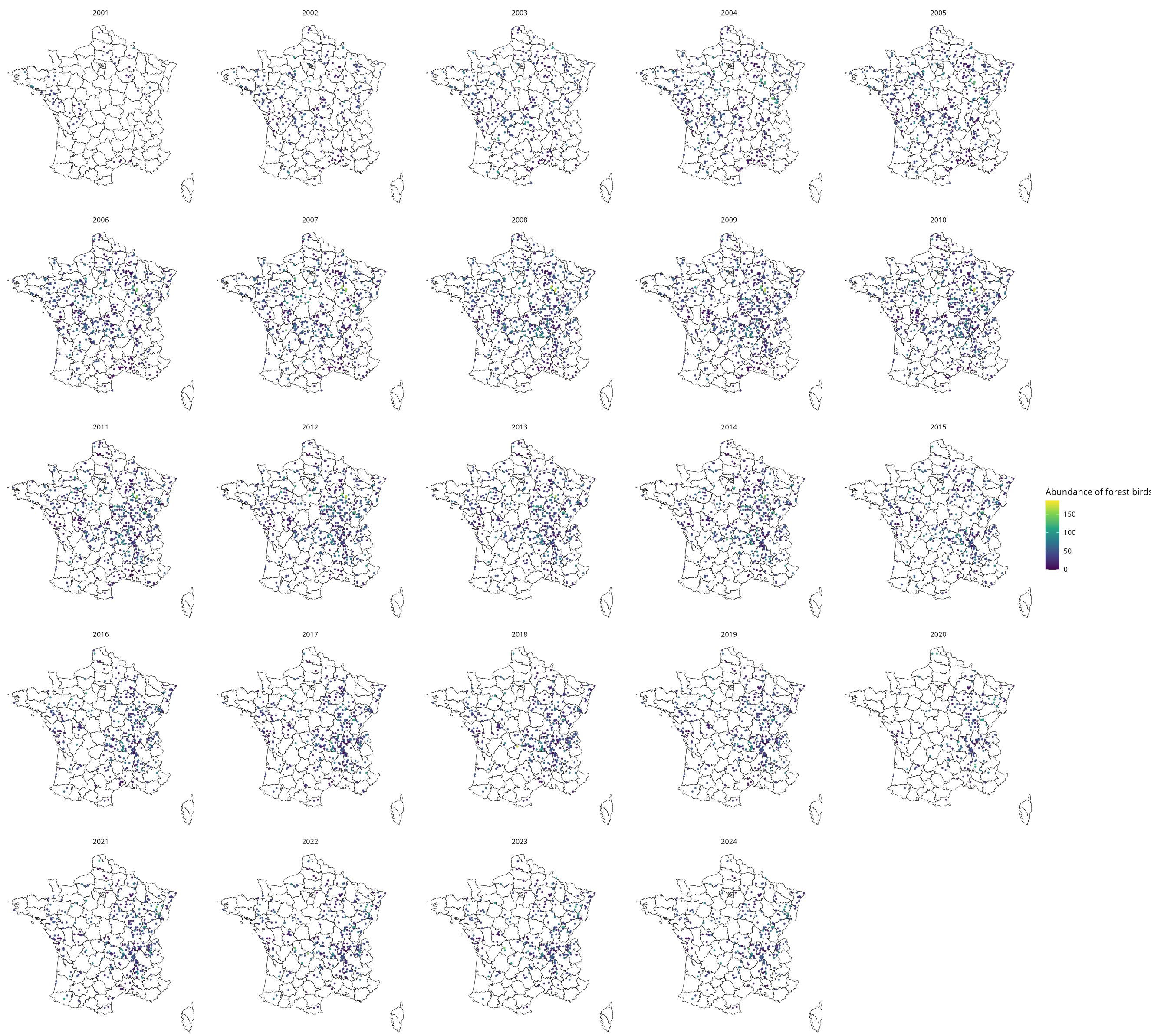

Figure SI-2: Abundance of forest birds observed in the STOC program, by year

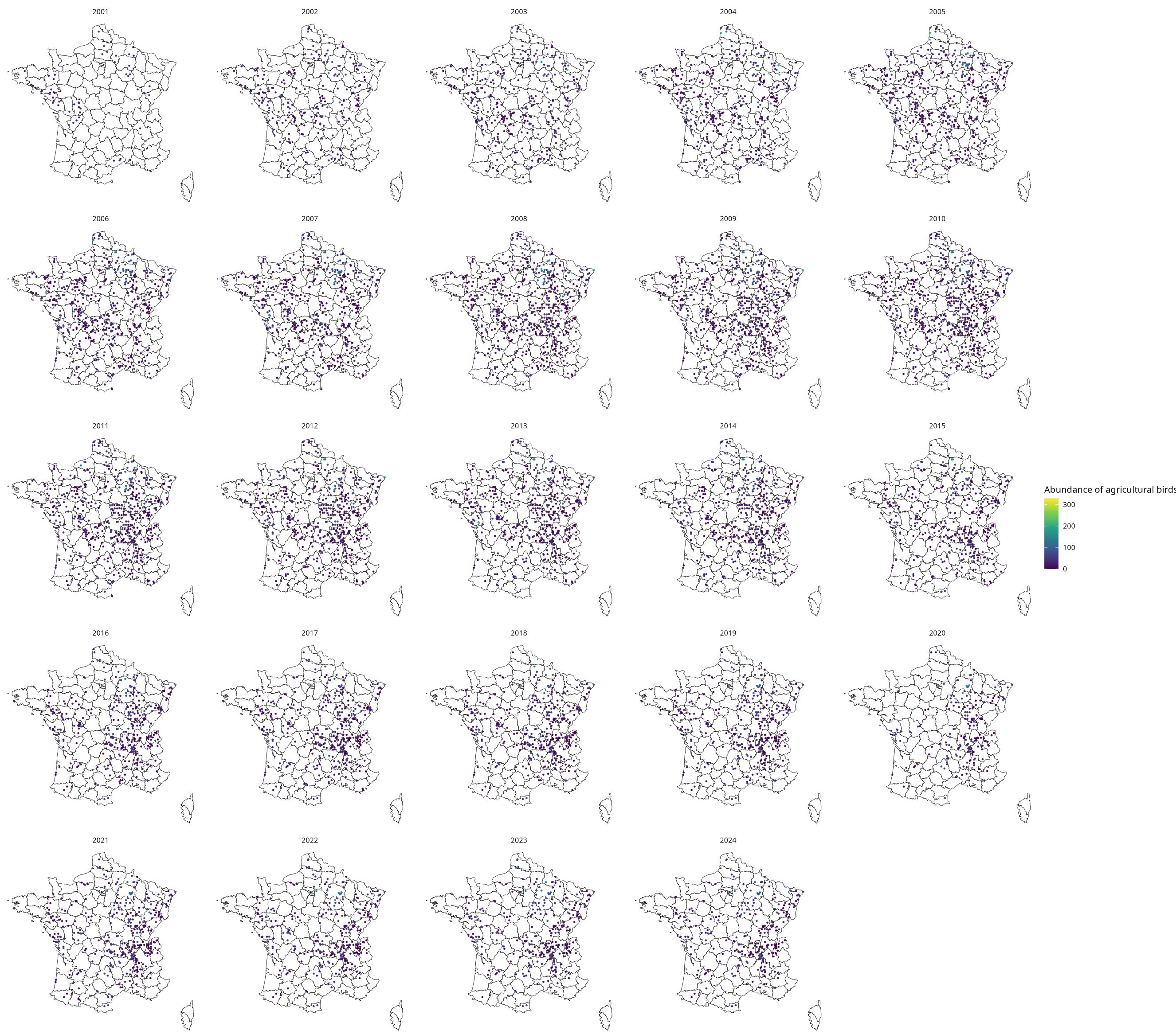

Figure SI-3: Abundance of agricultural birds observed in the STOC program, by year

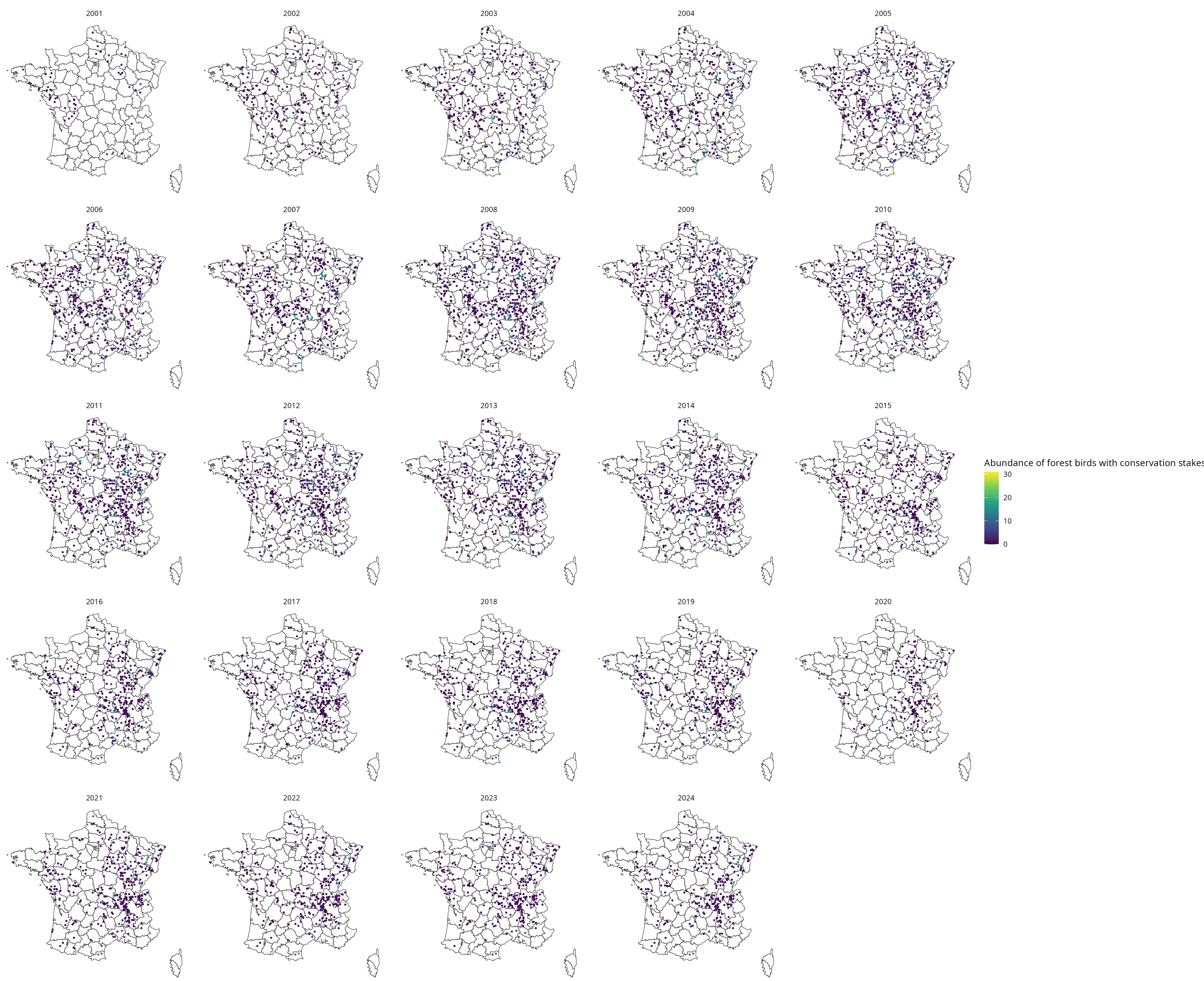

Figure SI-4: Abundance of forest birds with conservation stakes observed in the STOC program, by year

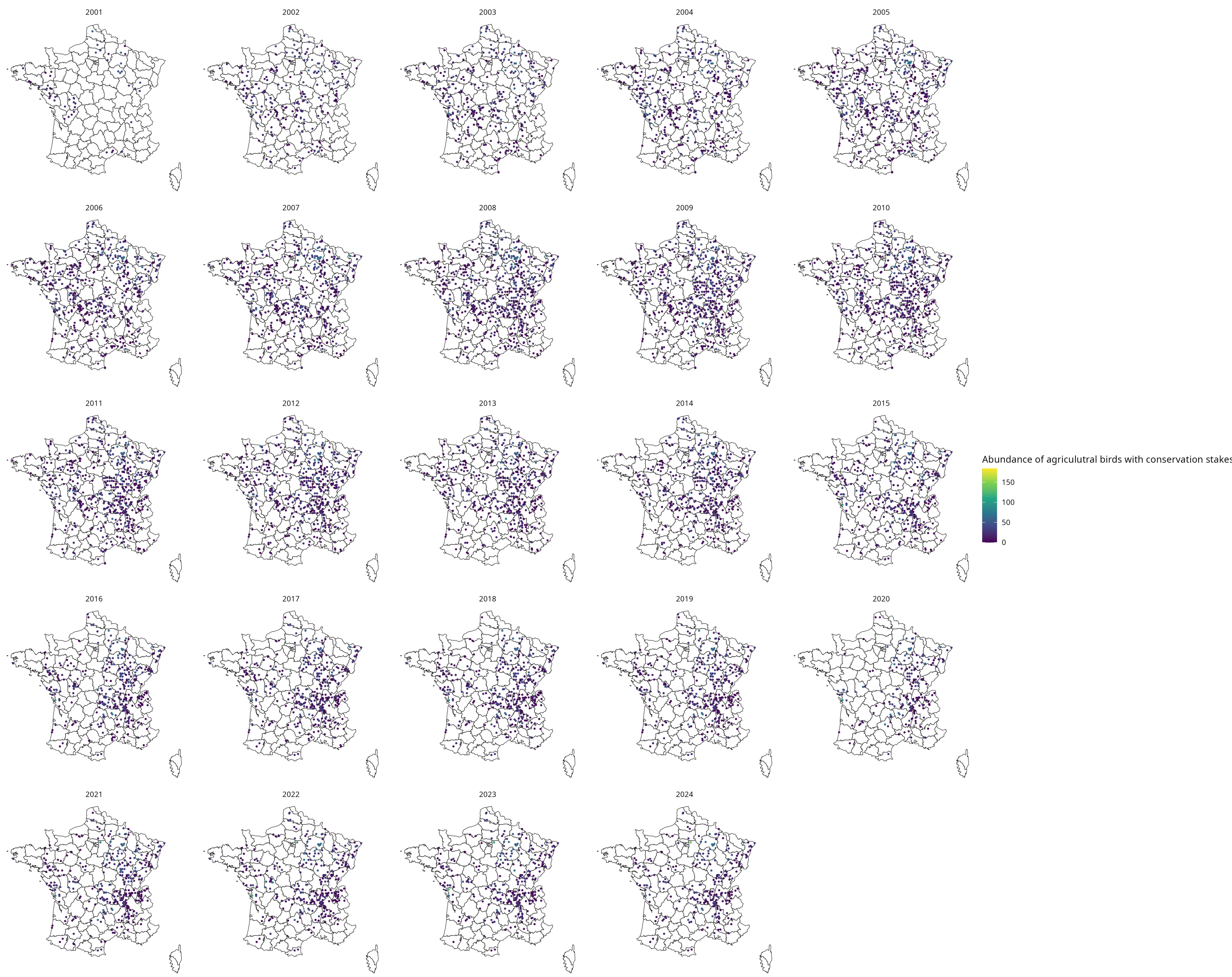

Figure SI-5: Abundance of agricultral birds with conservation stakes observed in the STOC program, by year

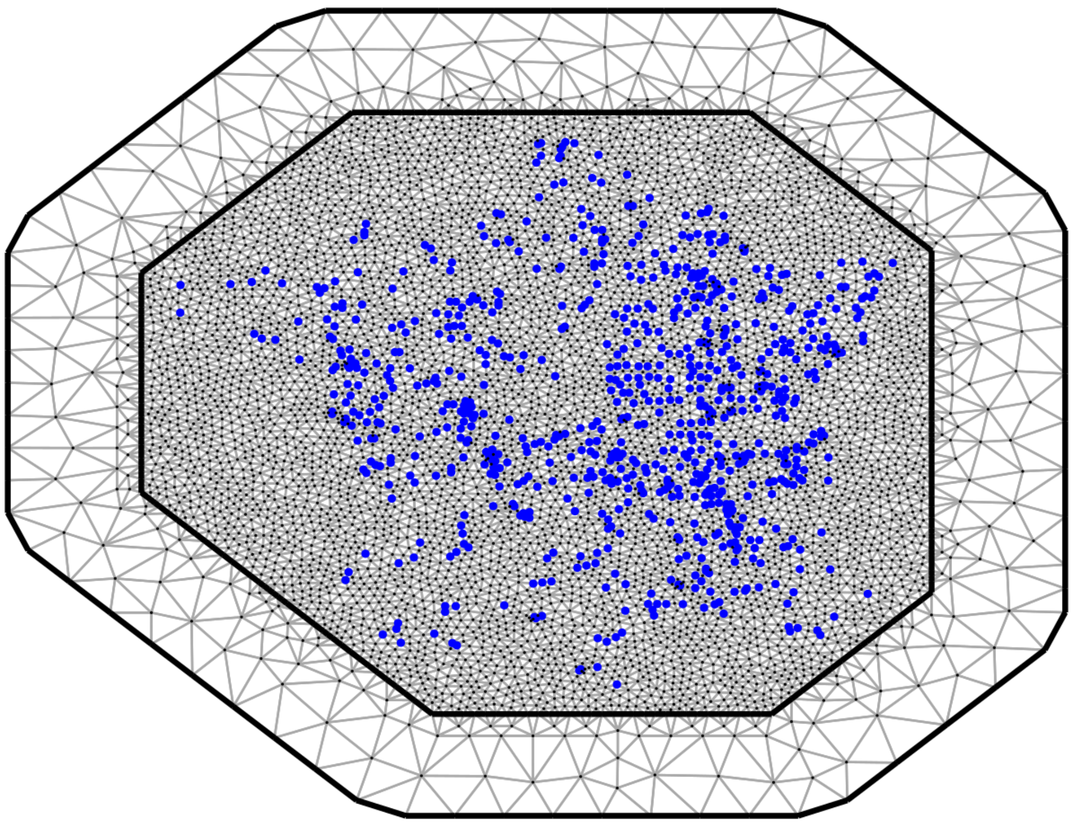

Figure SI-6: Mesh choice. The observed points are represented in blue.

	mean	sd	0.025quant	0.5quant	0.975quant	mode	kld
(Intercept)	1.45	0.05	1.36	1.45	1.55	1.45	0.00
latitude_cov	0.06	0.04	-0.01	0.06	0.13	0.06	0.00
tmax_last_spring	0.02	0.01	-0.00	0.02	0.04	0.02	0.00
tmax_last_summer	0.01	0.01	-0.01	0.01	0.03	0.01	0.00
Land1	-0.52	0.03	-0.58	-0.52	-0.46	-0.52	0.00
Land3	-0.23	0.02	-0.27	-0.23	-0.18	-0.23	0.00
surface_forest_10km	-0.03	0.04	-0.11	-0.03	0.04	-0.03	0.00
surface_243_10km	-0.05	0.03	-0.11	-0.05	0.01	-0.05	0.00
tmax_last_spring:surface_forest_10km	0.01	0.01	-0.00	0.01	0.03	0.01	0.00
tmax_last_summer:surface_243_10km	0.01	0.01	-0.00	0.01	0.02	0.01	0.00
latitude_cov:tmax_last_spring	0.02	0.01	0.01	0.02	0.03	0.02	0.00

	mean	sd	0.025quant	0.5quant	0.975quant	mode
(1/overdispersion)	11.64	0.28	11.09	11.64	12.21	11.64
Range for spatial (m)	17435.26	1365.42	14914.11	17377.90	20286.97	17255.39
Stdev for spatial	0.79	0.02	0.74	0.79	0.84	0.79
Precision for annee_factor	111.48	72.08	20.67	94.76	290.94	58.91
Rho for annee_factor	0.89	0.08	0.70	0.91	0.98	0.95

Table SI-2: agri

4 Corine Land cover Codes

CLC Code	**Class name**
111	Continuous urban fabric
112	Discontinuous urban fabric
121	Industrial or commercial units
122	Road and rail networks and associated land
123	Port areas
124	Airports
131	Mineral extraction sites
132	Dump sites
133	Construction sites
141	Green urban areas
142	Sport and leisure facilities
211	Non-irrigated arable land
212	Permanently irrigated land
213	Rice fields
221	Vineyards
222	Fruit trees and berry plantations
223	Olive groves

231	Pastures
241	Annual crops associated with permanent crops
242	Complex cultivation patterns
243	Land principally occupied by agriculture, with significant areas of natural vegetation
244	Agroforestry areas
311	Broad-leaved forest
312	Coniferous forest
313	Mixed forest
321	Natural grasslands
322	Moors and heath land
323	Sclerophyllous vegetation
324	Transitional woodland-shrub
331	Beaches, dunes, sands
332	Bare rocks
333	Sparsely vegetated areas
334	Burnt areas
335	Glaciers and perpetual snow
411	Inland marshes
412	Peat bogs
421	Salt marshes
422	Salines
423	Intertidal flats
511	Water courses
512	Water bodies
521	Coastal lagoons
522	Estuaries
523	Sea and ocean

Table SI-7: Corine Land Cover (CLC) Level 3 classification codes and class names

	mean	sd	0.025quant	0.5quant	0.975quant	mode	kld
(Intercept)	-0.48	0.12	-0.72	-0.48	-0.25	-0.48	0.00
latitude_cov	0.28	0.10	0.08	0.28	0.48	0.28	0.00
tmin_last_summer	-0.05	0.03	-0.12	-0.05	0.01	-0.05	0.00
tmax_last_spring	-0.08	0.03	-0.14	-0.08	-0.03	-0.08	0.00
tmax_last_summer	0.05	0.02	-0.00	0.05	0.09	0.05	0.00
Land1	0.78	0.05	0.67	0.78	0.88	0.78	0.00
Land2	0.08	0.04	0.01	0.08	0.16	0.08	0.00
shanon_nb_agri	-0.11	0.08	-0.26	-0.11	0.04	-0.11	0.00
surface_forest_10km	0.54	0.08	0.37	0.54	0.70	0.54	0.00
surface_243_10km	0.14	0.07	-0.00	0.14	0.28	0.14	0.00
tmax_last_summer:shanon_nb_agri	0.02	0.01	-0.01	0.02	0.04	0.02	0.00
tmax_last_spring:surface_forest_10km	0.02	0.02	-0.01	0.02	0.06	0.02	0.00
latitude_cov:tmax_last_spring	-0.05	0.02	-0.08	-0.05	-0.02	-0.05	0.00

	mean	sd	0.025quant	0.5quant	0.975quant	mode
(1/overdispersion)	12.87	1.47	10.24	12.78	16.00	12.60
Range for spatial (m)	36334.33	3889.39	29280.72	36127.94	44576.32	35719.07
Stdev for spatial	1.46	0.07	1.33	1.46	1.60	1.46
Precision for annee_factor	24.74	15.83	5.49	21.02	65.21	14.18
Rho for annee_factor	0.92	0.06	0.76	0.93	0.98	0.96

Table SI-3: C birds forest

	mean	sd	0.025quant	0.5quant	0.975quant	mode	kld
(Intercept)	1.70	0.02	1.66	1.70	1.75	1.70	0.00
Land1	0.44	0.02	0.40	0.44	0.49	0.44	0.00
Land2	-0.07	0.02	-0.10	-0.07	-0.04	-0.07	0.00
surface_243_10km	0.13	0.02	0.08	0.13	0.18	0.13	0.00
latitude_cov	0.23	0.03	0.17	0.23	0.30	0.23	0.00
surface_forest_10km	0.17	0.03	0.11	0.17	0.23	0.17	0.00
tmax_last_spring	-0.00	0.01	-0.02	-0.00	0.02	-0.00	0.00
tmax_last_summer	-0.01	0.01	-0.03	-0.01	0.01	-0.01	0.00
tmin_last_spring	0.03	0.01	0.01	0.03	0.04	0.03	0.00
surface_forest_10km:tmax_last_spring	-0.01	0.00	-0.02	-0.01	-0.01	-0.01	0.00
surface_forest_10km:tmax_last_summer	0.01	0.00	0.01	0.01	0.02	0.01	0.00

	mean	sd	0.025quant	0.5quant	0.975quant	mode
(1/overdispersion)	47.25	1.71	43.99	47.21	50.71	47.13
Range for spatial (m)	18336.21	1369.44	15796.14	18282.59	21185.06	18170.46
Stdev for spatial	0.72	0.02	0.68	0.72	0.76	0.72
Precision for annee_factor	367.41	156.77	132.08	343.02	735.57	294.44
Rho for annee_factor	0.60	0.16	0.26	0.62	0.86	0.65

Table SI-4: forest

	mean	sd	0.025quant	0.5quant	0.975quant	mode	kld
(Intercept)	2.25	0.03	2.19	2.25	2.30	2.26	0.00
Land1	0.03	0.01	0.01	0.03	0.06	0.03	0.00
shanon_nb_agri	0.15	0.01	0.12	0.15	0.17	0.15	0.00
latitude_cov	0.05	0.01	0.02	0.05	0.08	0.05	0.00
Land3	0.03	0.01	0.01	0.03	0.05	0.03	0.00

	mean	sd	0.025quant	0.5quant	0.975quant	mode
(1/overdispersion)	42.30	0.99	40.40	42.29	44.30	42.24
Range for spatial (m)	13071.93	1065.66	11080.66	13035.25	15273.40	12975.89
Stdev for spatial	0.39	0.01	0.36	0.39	0.42	0.39
Precision for annee_factor	359.25	243.30	67.33	300.15	980.45	185.71
Rho for annee_factor	0.89	0.08	0.69	0.91	0.98	0.95

Table SI-5: generalist