

Selection of Dynamic Models for Bird Populations in Farmlands

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Abstract Agricultural changes have caused severe decline in the common bird communities in Europe. Mitigating this loss requires both understanding of and way to predict how agriculture affects biodiversity. The objective of this paper is to test the different dynamic models coupling bird abundances with farming land use. The agro-ecological calibration relies on 2002–2009 data for 34 bird species and 14 agricultural systems in 620 small agricultural regions of metropolitan France. The models are compared based on indicators of goodness-of-fit and predictive quality. The results highlight the relevance of systemic, functional, and mechanistic relationships between the agriculture and bird populations in both descriptive and predictive contexts. However, it seems that the best dynamic models to describe the past trends are not necessarily the most relevant to predict the future trends although there is a similar subset of five models that emerges in both cases. Ranking these different models depends on both the objective (describing or predicting) and the chosen functional level for the analysis (total community, functional groups or species).

Keywords Agro-ecology · Bird · Model selection · Population dynamics · Intra-specific competition · Farming land-use · Adjustment · Prediction

1 Introduction

Many European countries have observed a strong decline in biodiversity in agricultural landscapes. This applies especially to mammals [1], arthropods and plants [2], and birds [3]. The common birds are particularly affected, and bird breeding surveys report significant loss of both abundance and diversity in many communities [4, 5]. Farmland birds are the most affected species: in France, there has been a 25 % loss in abundance over 20 years. Changes to agricultural practices over recent decades, and especially land use changes and intensification processes, have all been extremely detrimental [6]. The role played by grasslands and croplands has been studied in some depth [7–9]. The spread of mechanization, hedge cutting, habitat homogenization, and increased use of pesticides have all contributed to reducing bird survival rates and breeding success [5, 10], although no reduction in biodiversity has been found in high nature value farmland [11]. In the hope of reconciling productivity and biodiversity conservation on farmland, several scientific works examine the development of agricultural practices that are both economically and ecologically viable [12–15]. For instance, the European agro-environmental scheme offers national support to farmers who adopt environmentally-friendly practices. However, since most such schemes are not assessed for their cost-effectiveness, whether ecological, productive, and economic performance can be balanced remains an open question [16, 17].

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The development of multi-functional agriculture requires an understanding of the link between agriculture and biodiversity. In this context, agro-ecological models linking agriculture and biodiversity dynamics can be helpful. Similar to the climate change scenarios developed by the Intergovernmental Panel on Climate Change (IPCC)¹, models are needed to investigate the future global population and biodiversity patterns which will likely differ from historical trends in response to changes in agricultural practices [18–22].

These agro-ecological models have been used to describe the past trends and extrapolate time series into the future [23–25]. They are frequently based on statistical models, and techniques used to characterize time series and fit population models to time-series data. Statistical models analyze time series directly to produce descriptors of the dynamics involved. This method has some advantages: statistical techniques are well developed, especially in relation to the notion of “goodness of fit”, and use the mean squared error for both parameter estimation and comparison of the fit of different models to a particular data set. In considering the time series as a string of numbers, this approach requires few assumptions. In other words, these models tend to be biologically naive since they ignore qualitative and quantitative information about the underlying ecological system generating the time series. Such statistical analyses are not able to provide information about the underlying ecological mechanisms: there is no unique relationship between statistical patterns and mechanisms, and a particular pattern may be generated by a variety of mechanisms.

Independently, theoretical ecologists, going back to Lotka and Volterra, have identified a large number of mechanisms underlying population dynamics in ecosystems. The aim of theoretical approaches is typically to understand the causes of a generic phenomenon rather than a particular time series. These models are biologically explicit and take into account the processes driving the trajectories. While this approach increases our understanding of ecological processes—hence allowing predictions about the ecosystem in response to environmental changes—the model’s explanatory power is rarely evaluated on the basis of rigorous statistical goodness of fit.

In this context, statistical and mechanistic modeling approaches appear to be complementary. The goal of this paper is to develop agro-ecological models based on time series and ecological knowledge on population dynamics in order to obtain deeper insights into the biological mechanisms involved and to achieve more rigorous testing of the models that embody these mechanisms.

Many studies in the agro-ecological modeling literature focus on a particular landscape or a small number of

species [26–29]. However, a larger spatial scale (ecosystem, regional, national, and international) or a multi-scale approach leads to more informative results. Similarly, investigation of a large set of species rather than one or two emblematic species provides more robust and generic agro-ecological information. Birds are often used as a representative group [26, 27, 30–32]. They are frequently considered as a biodiversity compartment that is highly sensitive to agricultural patterns [5]. Also, a focus on breeding birds is justified because (i) birds are positioned at a high level in the trophic food chains and thus capture the variations in the chains; (ii) birds provide ecological services, such as regulation of invertebrate and rodent populations and pest control [33, 34]; (iii) their proximity to humans makes them a simple and comprehensive biodiversity index for a large audience of citizens [35].

The present paper develops dynamic models of bird populations affected by farming systems. In order to capture responses to agricultural pressures in bird population variations, these models link abundances of a large set (34) of common bird species to the utilized agricultural area (UAA) proportions dedicated to 14 agricultural patterns such as crop systems and bovine livestock breeding. These models are spatialized and calibrated over 620 French metropolitan small agricultural regions (SAR). Bird data for 2002–2009 were provided by the national French Breeding Bird Survey (FBBS), and agricultural data are taken from the Farm Accountancy Data Network (FADN), and the Observatory of Rural Development (ODR) databases. We test different models of population dynamics with different intra-specific competition. The comparison and selection of models rely on two criteria. First, adjustments to the data [23, 36]: the model has to fit the past time series. Second, predictive capacity [37, 38]: the model has to be able to predict abundance trends with moderate error such that they can be used for projections and scenarios.



Fig. 1 Maps of the Small Agricultural Regions (SAR)

¹www.ipcc.ch

Table 1 List of the 14 farming systems

The 14 farming systems

- (1) Cereal, Oleaginous, Proteaginous (COP)
- (2) Variegated crops
- (3) Intensive bovine livestock breeding
- (4) Medium bovine livestock breeding
- (5) Extensive bovine livestock breeding
- (6) Mixed crop-livestock farming with herbivorous direction
- (7) Other herbivorous livestock breeding
- (8) Mixed crop-livestock farming with granivorous direction
- (9) Mixed crop-livestock farming with other direction
- (10) Granivorous livestock breeding
- (11) Permanent farming
- (12) Flower farming
- (13) Viticulture
- (14) Others associations

2 Material and Methods

2.1 Data

The models are considered over 620 metropolitan French SAR² (Fig. 1). The homogeneity of SAR at both agronomic and ecological levels makes them particularly well-suited for our modeling. Historical agricultural data for these regions are from the Farm Accountancy Data Network and the Observatory of Rural Development.³ They identify 14 agricultural systems detailed in Table 1. The surfaces dedicated to each agricultural system in every SAR are available between 2001 and 2008 on the ODR website.

The ecological part of the model is based on 2002–2009 data for France provided by the national FBBS. Among the common breeding species monitored, we focus on the 34 species (Table 2) classified by the FBBS⁴ as farmland specialist and habitat generalist species in line with the method in [39]. Published abundance values for each species are available for the period 2002–2009 as detailed in [30] and in [40].⁵

²Although there are 713 SAR in France, we have both ecological and agricultural data only for 620 of them in metropolitan France (Corsica excluded).

³<http://ec.europa.eu/agriculture/rica>

⁴see in <http://vigienature.mnhn.fr/page/oiseaux>

⁵Abundance values for each species were available for the period 2002–2009 for 1747 squares (a square is 2 × km in size) (as detailed in [40]). For each species, [30] further performed a spatial interpolation of these abundance data to obtain relative abundance values for each possible square in the country (e.g., 136,000 squares) using kriging models based on spatial autocorrelation and an exponential function. The abundance values are averaged at the PRA scale to calibrate the ecological model.

2.2 Bird Dynamics

Six functional forms are described in discrete time. Each model is defined for each species *s* at national scale using data at the SAR scale *r* for their calibration. The variable $N_{s,r}(t)$ stands for the abundance of species *s* in SAR *r* at year⁶ *t*.

- **Model BH:**

$$N_{s,r}(t + 1) = N_{s,r}(t) \frac{1 + R_s}{1 + \frac{N_{s,r}(t)}{M_{s,r}(t)}}, \tag{1}$$

where the habitat quality $M_{s,r}(t)$ is characterized by

$$M_{s,r}(t) = b_s + \sum_{k=1}^{14} a_{s,k} A_{r,k}(t). \tag{2}$$

The model BH in equation (1) refers to the Beverton-Holt dynamics [41]. It includes an intra-specific competition, with a carrying capacity $K_s(t) = R_s * M_{s,r}(t)$ where R_s corresponds to the growth rate and $M_{s,r}(t)$ corresponds to the habitat value. The variable $M_{s,r}(t)$ is built as an affine function of the proportions $A_{r,k}(t)$ of the UAA dedicated to the agricultural system *k* in the SAR *r* at time *t*. The coefficient $a_{s,k}$ corresponds to the response of the species *s* to this agricultural system *k*. The parameter b_s captures the effect of all other habitats: the other agricultural systems and the non-agricultural land-use including forests and cities. This Beverton-Holt model is an example of the contest competition, which implies that one part of the population (the winners) dominates the other part (the losers) in the sense that only the former will survive if

⁶“At year *t*” means at the mid of year *t* because bird data are collected each year by May-June.

Table 2 The lowest Root Mean Square Errors (RMSE) in and out of sample for each species with the name of the optimal model among the 12 tested models

Species	Habitat	$RMSE_{in}$	Model	$RMSE_{out}$	Model
(1) Buzzard <i>Buteo buteo</i>	Specialist	55.78	LO	70.88	LO
(2) Cirl Bunting <i>Emberiza cirulus</i>	Specialist	60.62	RI	77.09	RI
(3) Corn Bunting <i>Emberiza calandra</i>	Specialist	47.22	RI	56.74	RI
(4) Grey Partridge <i>Perdrix perdrix</i>	Specialist	46.43	GO	89.63	GO
(5) Hoopoe <i>Upupa epops</i>	Specialist	13.50	LO	14.76	BH
(6) Kestrel <i>Falco tinnunculus</i>	Specialist	45.44	BH	56.95	BH
(7) Lapwing <i>Vanellus vanellus</i>	Specialist	23.11	BH	22.32	BH
(8) Linnet <i>Carduelis cannabina</i>	Specialist	216.50	BH	198.40	BH
(9) Meadow Pipit <i>Anthus pratensis</i>	Specialist	78.85	BH	116.00	RI
(10) Quail <i>Coturnis coturnis</i>	Specialist	30.98	BH	35.57	LO_5
(11) Red-backed Shrike <i>Lanius collurio</i>	Specialist	25.86	LO	36.97	LO
(12) Red-legged Partridge <i>Alectoris rufa</i>	Specialist	35.06	BH	37.39	BH
(13) Rook <i>Corvus frugilenus</i>	Specialist	210.97	LO	226.86	BH
(14) Skylark <i>Alauda arvensis</i>	Specialist	108.96	LO_5	174.35	LO_5
(15) Stonechat <i>Saxicola torquatus</i>	Specialist	55.11	RI	65.98	LO
(16) Whinchat <i>Saxicola rubetra</i>	Specialist	11.99	BH	16.96	RI
(17) Whitethroat <i>Sylvia communis</i>	Specialist	66.44	RI	86.06	LO_5
(18) Wood Lark <i>Lullula arborea</i>	Specialist	19.70	LO_5	24.14	LO_5
(19) Yellowhammer <i>Emberiza citrinella</i>	Specialist	61.04	LO_5	72.33	LO_5
(20) Yellow Wagtail <i>Motacilla flava</i>	Specialist	31.95	RI	40.35	RI
(21) Blackbird <i>Turdus merula</i>	Generalist	114.20	GO	200.31	LO
(22) Blackcap <i>Sylvia atricapilla</i>	Generalist	151.45	GO	211.32	GO
(23) Blue Tit <i>Parus caeruleus</i>	Generalist	202.24	GO	295.78	RI
(24) Carrion crow <i>Corvus corone</i>	Generalist	170.71	GO	205.83	GO
(25) Chaffinch <i>Fringilla coelebs</i>	Generalist	181.86	RI	254.13	RI
(26) Cuckoo <i>Cuculus canorus</i>	Generalist	44.28	LO_5	50.88	LO_5
(27) Dunnock <i>Prunella modularis</i>	Generalist	57.74	BH	75.65	RI
(28) Great Tit <i>Parus major</i>	Generalist	136.10	GO	181.51	GO
(29) Green Woodpecker <i>Picus viridis</i>	Generalist	50.83	RI	70.33	BH
(30) Golden oriole <i>Oriolus oriolus</i>	Generalist	37.79	RI	45.71	BH
(31) Jay <i>Garrulus glandarius</i>	Generalist	78.11	GO	93.64	BH
(32) Melodious Warbler <i>Hippolais polyglotta</i>	Generalist	37.79	LO	42.55	RI
(33) Nightingale <i>Luscinia megarhynchos</i>	Generalist	63.18	LO_5	131.91	GO
(34) Wood Pigeon <i>Columba palumbus</i>	Generalist	106.30	GO	147.70	LO_3

resources are lacking [42, 43]. This competition is an interference competition implying aggression and contest between individuals. When the initial abundance is above the carrying capacity, the population declines gradually towards the equilibrium due to the decrease of the losers. This model was originally introduced in the context of fisheries.

- **Model GO:**

$$N_{s,r}(t+1) = N_{s,r}(t) \exp \left[R_s \left(1 - \frac{\log(N_{s,r}(t))}{\log(R_s M_{s,r}(t))} \right) \right], \quad (3)$$

where $M_{s,r}(t)$ is defined as in Eq. 2. A contest competition underlies this Gompertz GO model similarly to the BH model. The gradual decline of the population towards the equilibrium is slower than the case of Beverton-Holt dynamics.

- **Model RI:**

$$N_{s,r}(t+1) = N_{s,r}(t) \exp \left[R_s \left(1 - \frac{N_{s,r}(t)}{R_s M_{s,r}(t)} \right) \right], \quad (4)$$

where $M_{s,r}(t)$ is defined as in Eq. 2. The Ricker model RI (Eq. 4) describes another density-dependence relation. The Ricker relation captures a scramble

competition: resources are equally divided among all individuals [42, 43] and whenever the population rises above its carrying capacity, the abundance first collapses then returns to its equilibrium. The scramble competition is an exploitative competition based on adjustments of ranging behavior to group size, including home-range size and daily travel distance. This kind of competition has been identified among beetles [44] and in Lepidopteran butterflies [45].

• **Model LO:**

$$N_{s,r}(t+1) = N_{s,r}(t) + N_{s,r}(t) R_s \left(1 - \frac{N_{s,r}(t)}{R_s M_{s,r}(t)} \right). \quad (5)$$

The logistic model LO is a different functional form of the scramble competition. After an initial collapse, the population returns to the equilibrium but more slowly than described by the Ricker model.

• **Model BH_θ:**

$$N_{s,r}(t + 1) = N_{s,r}(t) \frac{1 + R_s}{\left(1 + \frac{N_{s,r}(t)}{M_{s,r}(t)} \right)^\theta}, \quad (6)$$

with $\theta > 1$ and where $M_{s,r}(t)$ is defined as in equation (2). This model reinforces the role played by the density-dependence through the parameter θ [46, 47]. The variable θ characterizes the type and intensity of density dependence. The competition corresponds also to a scramble competition [42] but adding intensity θ leads to steady populations that are smaller than with BH models for a given set of parameters. Moreover, the convergence towards the equilibrium after the first collapse is very fast. In order to retain the same number of estimated parameters as in the previous models, the value of θ is set before calibration.

• **Model LO_θ:**

$$N_{s,r}(t + 1) = N_{s,r}(t) + N_{s,r}(t) R_s \left[1 - \left(\frac{N_{s,r}(t)}{R_s M_{s,r}(t)} \right)^\theta \right], \quad (7)$$

with the intensity of competition $\theta > 1$ and where $M_{s,r}(t)$ is defined as in Eq. 2. Based on the logistic form, this model also fosters the role played by density-dependence, similar to the BH_θ model. In these models, the strength of the competition is limited for small populations and increases strongly with population size [46]. In contrast to the BH_θ models, the equilibrium in the LO_θ models is the same as with the LO model. However, similarly to the BH_θ models, the convergence towards the equilibrium after the first collapse is also very fast. The value of intensity θ is also set before calibration.

2.3 Model Evaluations

2.3.1 Calibration

For each species, the six functional forms are calibrated using a least square method used to estimate the set of parameters that minimizes the root mean square error (RMSE) of calibration computed on the time series $[t_1, t_2]$:

$$\min_{R_s; b_s; a_{s,k}} RMSE_s(t_1, t_2), \quad (8)$$

where the calibration error $RMSE_s(t_1, t_2)$ is defined as follows:

$$RMSE_s(t_1, t_2) = \sqrt{\frac{\sum_{t=t_1}^{t_2} \sum_{r=1}^{620} (\widehat{N_{s,r}(t)} - N_{s,r}(t))^2}{620 * (t_2 - t_1 + 1)}}. \quad (9)$$

Here, $N_{s,r}(t)$ represents the historical abundances of species s in SAR r while $\widehat{N_{s,r}(t)}$ corresponds to the abundances estimated by the model. In order to test both the goodness-of-fit and the predictive qualities of a calibration set, we split the data into 2002–2005 and 2006–2009 subsets. The model calibration is thus based on the years 2002–2005. Then we evaluate the goodness-of-fit on this time series. The predictive power of the calibration set is evaluated with the 2006–2009 time series. Values $\theta = 2, 3, 4, 5$ are tested for models BH_θ and LO_θ, resulting in a set of 12 tested models. We use the *datafit* function of Scilab software⁷. This function takes the initial historical populations $N_{s,r}(2002)$ as the starting populations and estimates all the years recursively between 2003 and 2009 based on the models.

2.3.2 Model Selection

The objective is to evaluate the capacity of the above models to describe the current bird populations trajectories and predict future trends. To estimate the quality of the calibration and the predictive power of the different models, we compare the RMSE in and out sample for each species. The $RMSE_{in}$ is computed using the data sample which was used for the estimation; $RMSE_{out}$ is based on out-of-sample data. More precisely, we compute the $RMSE_{in}$ with $t_1 = 2003$ ⁸ and $t_2 = 2005$, and the $RMSE_{out}$ with $t_1 = 2006$ and $t_2 = 2009$. The RMSE provides information on the mean error with respect to the calibration point in terms of bird abundances. Since the RMSE represents an absolute deviation which does not take account of the size

⁷It relies on an optimization algorithm of conjugate gradients [48]. Free software for scientific computation: <http://www.scilab.org/>

⁸The historical and calibrated are identical by definition at the starting year: in other words, year 2002 does not affect the evaluation of the quality of the calibration.

Table 3 The Mean Absolute Percentage Error MAPE (in percent) for the 12 models within the two functional groups and the total community based on the 34 species

	Specialist group		Generalist group		Total	
	$MAPE_{in}$	$MAPE_{out}$	$MAPE_{in}$	$MAPE_{out}$	$MAPE_{in}$	$MAPE_{out}$
BH	21.3	10.6	21.3	29.7	21.3	18.5
GO	∞	∞	∞	∞	∞	∞
RI	15.3	15.4	4.7	7.4	11.0	12.1
LO	15.5	15.6	8.6	13.3	10.0	14.2
BH2	∞	∞	∞	∞	∞	∞
BH3	60.5	37.9	227	279	129	137
BH4	60.5	37.9	228	279	129	137
BH5	60.5	37.9	228	279	129	137
LO2	∞	∞	∞	∞	∞	∞
LO3	59.4	44.5	198	148	116	87.3
LO4	∞	∞	∞	∞	∞	∞
LO5	16.2	16.8	2.8	5.4	10.7	12.1

of the population, this criteria displays strong differences between species.

2.3.3 Species Comparison

To compare the species or to aggregate them into average performance for the specialist versus generalist group, or the total community, we complete the RMSE by the Mean Absolute Percentage Error (MAPE). The MAPE represents the average of the absolute values of the percentage errors:

$$MAPE_s(t_1, t_2) = \frac{1}{620 * (t_2 - t_1 + 1)} \sum_{t=t_1}^{t_2} \sum_{r=1}^{620} \left| \frac{\widehat{N_{s,r}(t)} - N_{s,r}(t)}{N_{s,r}(t)} \right|. \tag{10}$$

Similarly to the RMSE, the in-sample analysis is based on $t_1 = 2003$ and $t_2 = 2005$ while the out-sample analysis relies on $t_1 = 2006$ and $t_2 = 2009$.

We estimate an average MAPE over the groups G based on the total community (i.e., $Card(G) = 34$), the farmland specialist species (i.e., $Card(G) = 20$) and generalist species (i.e., $Card(G) = 14$) as an arithmetic mean:

$$MAPE(t) = \frac{1}{Card(G)} \sum_{s \in G} MAPE_s(t). \tag{11}$$

3 Results

3.1 Goodness-of-fit

For the 34 species, column 3 in Table 2 presents the lowest Root Mean Square Error based on in-sample data $RMSE_{in}$

and the name of the associated model on the fourth column. This indicator represents the deviation of the calibration on the abundances at the SAR scale.⁹ According to the set of tested models, five functional forms show better performance in describing the past dynamics of the 34 studied species: BH, RI, LO, GO, LO₅.

Based on aggregate criteria, the analysis of the $MAPE_{in}$ (Table 3) shows that RI, LO, and LO₅ are the best models although the three indicators (based on the total community, the specialist group, and the generalist group) do not rank them in the same way.

Using the goodness-of-fit namely the $RMSE_{in}$, Fig. 2 compares national historical and estimated abundances in the whole 2002–2005 time series both for the specialist and the generalist groups (to avoid dominance of high abundance species, we display relative abundances $\frac{N_i(t)}{\sum_{t'=2002}^{2005} N_i(t')}$). The estimated abundances are computed using the best model per species (see Table 2). The position of the crosses on the diagonal points to a satisfactory goodness-of-fit for the 34 species.

The adjustment is depicted in Fig. 3 which shows 12 examples of calibrations (six specialist and six generalist species) plotting historical abundances (dotted line), estimated abundances based on the optimal models (black thick line), and the 95 % confidence intervals of the calibration error (thin lines). These examples show that the estimated

⁹Since the indicator is sensitive to the population size, it is possible to compare the performances of the different models for one species, but it shall not be used to compare the species.

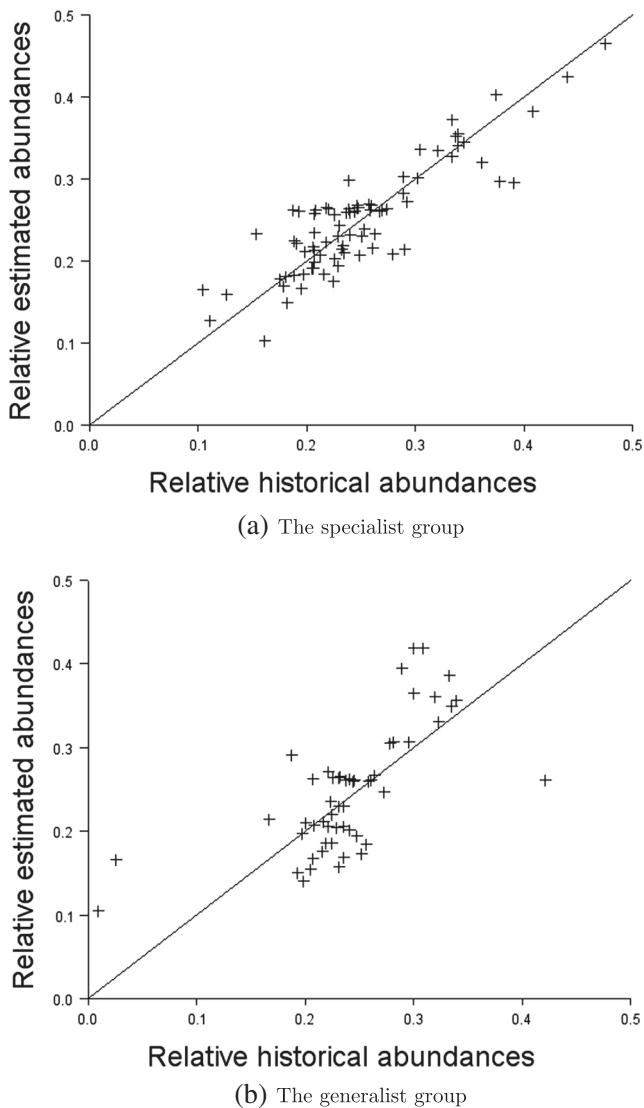


Fig. 2 Comparison between national relative historical and estimated abundances with the best model (see Table 2) in the 2002–2005 time series for the 20 farmland specialist and the 14 habitat generalist species

dynamics fit with the historical paths although it requires some smoothing of the inter-annual variations.

3.2 Prediction

Columns 5 and 6 in Table 2 describe the best $RMSE_{out}$ of the 34 species. These performances are higher than for the $RMSE_{in}$, suggesting that the goodness-of-fit is better quality than the prediction for the same calibration set. Analysis of the $RMSE_{out}$ confirms the dominance of the five models (BH, RI, LO, GO, and LO_5) to predict the population dynamics.

The analysis of the $MAPE_{out}$ (Table 3) shows that RI, LO_5 , and BH are the best models although the three indicators (for total community and specialist and generalist

groups) rank them differently, similarly to the case of the goodness-of-fit analysis.

Figure 4 compares 2006–2009 national relative historical and the predicted abundances both for the specialist and the generalist groups (similar to Fig. 2, relative abundances are written as $\frac{N_i(t)}{\sum_{t'=2006}^{2009} N_i(t')}$). The predicted abundances are computed using the best predictive model for the species (see Table 2). Although the dispersion is slightly higher than in Fig. 2, the crosses are still close to the first diagonal, which emphasizes a satisfactory adjustment for the 34 species.

4 Discussion

4.1 The Interest of Mechanistic Models for Agro-ecology

To complement the theoretical studies [49], models of population dynamics can be exploited in a more applied framework to mimic past trajectories in response to different pressures [3, 23, 50]. A unique contribution of this paper is that it proposes mechanistic, dynamic, and systemic models in an agro-ecological context, as opposed to the more widespread statistical models [5, 11, 24]. These mechanistic models are based on functional responses whereas statistical models are based on correlations. Analysis of these models based on the classical statistical root mean square error criteria confirms the relevance of a mechanistic and systemic modeling to describe bird populations on farmlands.¹⁰ Our study goes a step further and proposes an evaluation of these calibrated models according to their predictive capacity. This assessment is crucial from the perspective of developing biodiversity scenarios [20, 33, 51, 52] similar to the climate change scenarios developed within the IPCC¹¹ framework.

Specifically, we highlighted that, whatever the objective (describe or predict), there is convergence towards a small set of models to describe the population dynamics of birds on farmland. Among the 12 models tested, five models emerge as useful: the Ricker, Beverton-Holt, Gompertz, logistic, and generalized logistic $\theta = 5$. However, ranking these five models is not trivial. In particular, we showed the crucial role played by the functional level chosen for the analysis, that is, the entire community, the functional group (specialist and generalist groups), or the species. The ranking of these five models depends heavily on the functional

¹⁰Other models (as polynomial functions) could fit well with the data. It would be a different approach, which will not give the same information than the mechanistic approach and could be complementary as detailed in the introduction. It also could be informative to compare statistical and mechanistic approaches but it is beyond the scope of this article.

¹¹www.ipcc.ch

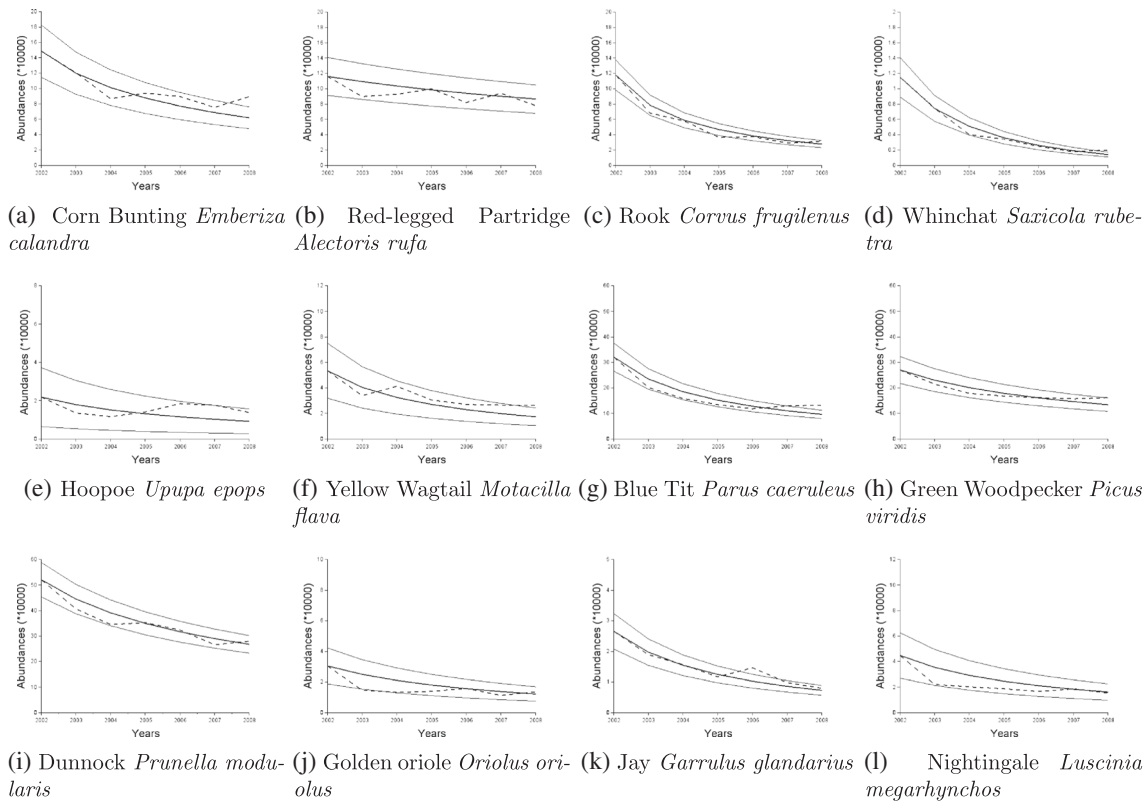


Fig. 3 Examples of calibration comparing the historical (*dotted line*), the estimated (*solid line*) national abundances with the optimal model and the 95 % confidence interval (*thin lines*) for six specialist species (**a–f**) and 6 generalist species (**g–l**)

level (see Table 4). This suggests that the average conclusion on an agglomerated scale (functional group or community) does not emerge from the average trend at a lower functional level. On the contrary, behaviors at the species scale differ greatly amongst species. In addition to the classical debate related to the model goal (describe or predict), we point out that the functional level analyzed for analysis is also decisive for model selection.

4.2 Describe Versus Predict

The contrasting patterns between the in-sample and out-sample analysis (based on RMSE and MAPE) underline the difficulty involved in designing models able to both describe and predict population dynamics within the same model using the same calibration set. However, our study highlights two general trends which are independent of the model goal.

First, we showed that refining the functional level of the analysis emphasizes the positive role of the Beverton-Holt and the Gompertz models, whatever the objective (describe or predict). Although they are not the most efficient in the aggregated analysis, at the species level they are dominant in the in- and out-sample analysis. This is interesting since both models represent a contest competition whereas the

other 10 models depict a scramble competition. The contest competition implies that a part of the population dominates the other part in the sense that only the former will eventually survive if resources are lacking [43]. Thus, when the initial abundance is above the carrying capacity, the population declines gradually towards the equilibrium. The selection of this kind of competition on French data at the species scale is consistent with others species-based studies in Europe which suggest progressive degradation of farmland bird populations in response to agricultural variables. For instance, in Sweden, during the period 1976–2003, [53] observed progressive decline in four migratory species which coincided with major agricultural policy changes. Similarly in England, bird populations decreased progressively in the 1970s as a result of the spread of intensive agriculture [3, 24, 25].

Second, we highlighted a balance between environmental drivers and biological traits. Amongst the 34 tested species, only 5 (7 resp.) are associated with a model with a high θ in the in-sample (out-sample resp.) analysis. A high level of θ indeed fosters the convergence towards carrying capacity, thus emphasizing the role played by habitat at the expense of the intrinsic growth rate. In our case, as most of the species are characterized by a low value of θ , a balance is required between the growth R and habitat M parameters to

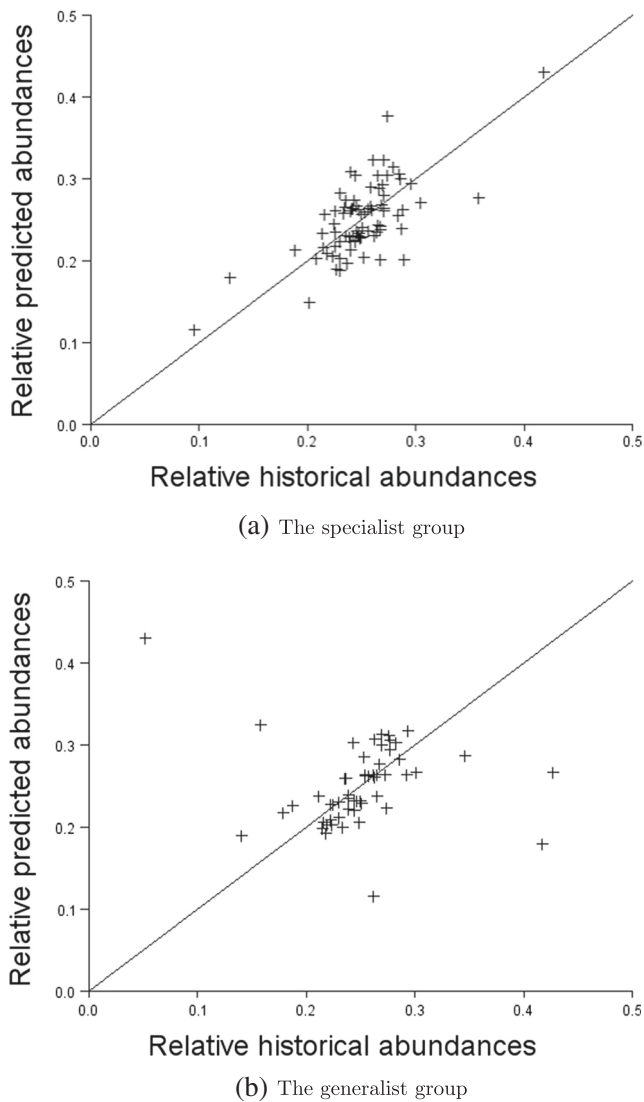


Fig. 4 Comparison between national relative historical and predicted abundances with the predictive models (see Table 2) in 2006–2009 for the 20 farmland specialist and the 14 habitat generalist species

understand bird populations in farming landscapes in relation to both description and prediction. In other words, a

fine adjustment to the agricultural variables affecting habitat quality and other traits is required to improve the calibration. This is consistent with various studies which highlight the impact of other environmental variables on population dynamics such as pollution [54, 55] and climate change [18, 56, 57]. These variables affect bird populations notably through the nesting success [6]. With a view to improving the models, other drivers should be examined more explicitly. In particular, other environmental drivers and biological traits including inter-specific competition, regional dispersion, or evolution of geographic range in response to climate change should be combined with new land uses such as forest or urban areas.

4.3 Limits and Perspectives

The models presented in this paper rely on coupling data on bird populations and land use. These databases provide many details: (i) they are collected at a small spatial scale for the whole country which allows large scale studies that retain regional specificities; (ii) they monitor many bird species which allows for a community approach to biodiversity not restricted to one emblematic species; and (iii) they provide annual time series for both bird and land use which are essential to build dynamic processes and adopt an ecosystem perspective.

However, our study has some limitations. First, the time series covers a limited period (in our case 2002–2009) which reduces the genericity of our results. This points to the importance of maintaining and developing the French Breeding Bird Survey. An expanded database would allow refinements to the calibration of the models which would increase their quality. This would allow the results of the present study to be tested. In addition to an extended time series, extension to the European scale would provide major insights into the drivers of functional responses to terrestrial biodiversity. Second, at this stage, the models cannot account for spatial dispersion between SAR; consequently, populations starting from zero remain equal to zero.

Table 4 Rankings of the models according to the functional level (total community $MAPE_{tot}$, functional group $MAPE_{spe}$ and $MAPE_{gen}$, species $RMSE$) and the objective (describe with the in-sample and predict with the out-sample)

	In-sample	Out-sample
$MAPE_{tot}$	$L0 > L0_5 > RI > BH$	$RI = L0_5 > LO > BH$
$MAPE_{spe}$	$RI > L0 > L0_5 > BH$	$BH > RI > LO > L0_5$
$MAPE_{gen}$	$L0_5 > RI > LO > BH$	$L0_5 > RI > LO > BH$
Spe based on $RMSE$	$BH > RI > LO > L0_5$	$BH > L0_5 = RI > LO$
Gen based on $RMSE$	$GO > RI > L0_5$	$GO = RI > BH$
Tot based on $RMSE$	$BH = GO = RI > L0_5 = LO$	$BH = RI > L0_5 > GO > RI$

We made three counts for the $RMSE$ analysis (based on the two functional groups and on the total community) in order to compare the results with the agglomerate indicator $MAPE$

Meta-population models would allow major improvements to predictions about the relevance of ecological processes, especially within the context of climatic change and changing ecological niches.

Finally, our study proposes a different way to analyze farmland bird species. Farmland bird species are currently classified according to many criteria (habitat specialization, trophic level, and specialization degrees) but a complementary classification based on a functional feature—intra-specific competition (contest versus scramble)—could be investigated. Based on species analysis, we observe two groups of species based on contest and scramble competitions: 16 contest species versus 18 scramble species for the in-sample indicator, and 14 contest species versus 20 scramble species for the out-sample indicator. Repartition of the species within these two groups does not fit with the specialization classification (specialist versus generalist). Further research in this area could add to our understanding of farmland birds.

5 Conclusion

In developing mechanistic, dynamic, and systemic models, this study has stressed the interest of functional responses between agricultural features and bird populations which previously have been investigated through correlative and statistical relations [5, 11, 16, 53]. We also compared the descriptive and predictive indicators and showed that models relevant for mimicking historical dynamics are not necessarily best-suited to extrapolating future trajectories. Some caution is needed when using descriptive models for prediction, projections, and scenarios. We show also that the model choice depends strongly on the functional level. The functional level used in the analysis is as important as the objective (describe or predict).

List of Acronyms

BH	Beverton-Holt,
FADN	Farm Accountancy Data Network,
FBBS	French Breeding Bird Survey,
GO	Gompertz,
LO	logistic,
MAPE	mean absolute percentage error,
ODR	Observatoire du Développement Rural,
RI	Ricker,
RMSE	root mean square error,
SAR	small agricultural region,
UA	utilized agricultural area.

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