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Integrated models, scenarios and dynamics of climate, land use and common birds

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Abstract Reconciling food, fiber and energy production with biodiversity conservation is among the greatest challenges of the century, especially in the face of climate change. Model-based scenarios linking climate, land use and biodiversity can be exceptionally useful tools for decision support in this context. We present a modeling framework that links climate projections, private land use decisions including farming, forest and urban uses and the abundances of common birds as an indicator of biodiversity. Our major innovation is to simultaneously integrate the direct impacts of climate change and land use on biodiversity as well as indirect impacts mediated by climate change effects on land use, all at very fine spatial resolution. In addition, our framework can be used to evaluate incentive-based conservation policies in terms of land use and biodiversity over several decades. The results for our case study in France indicate that the projected effects of climate change dominate the effects of land use on bird abundances. As a conservation policy, implementing a spatially uniform payment for pastures has a positive effect in relatively few locations and only on the least vulnerable bird species.

Keywords Integrated models · land use · incentive policy · common birds

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1 Introduction

Climate and land use changes are considered to be two of the main drivers of past and future variations in terrestrial biodiversity (MEA 2005, Pereira et al. 2010; Willis and MacDonald 2011). For medium-term projections (ca. 40 yrs into the future) these two drivers can be treated very differently in terms of scenarios and possibilities of intervention for biological conservation policy (de Chazal and Rounsevell 2009; Wintle et al. 2011). Global warming depends on international commitments to reduce greenhouse gas emissions, and much of the climate change projected over the next four decades is already committed due to long lag times socio-economic drivers and in the Earth system (IPCC 2013). By contrast, Land Use Changes (LUC) are potentially under much greater control of national and local decision makers concerning impacts on biodiversity over the next few decades (Schröter et al. 2005; Verburg et al. 2008 but see Radeloff et al. 2012).

However, present and future land uses are influenced by climate change, and this is rarely accounted for when exploring the interactive effects of climate change and land use on biodiversity (de Chazal and Rounsevell 2009). Local opportunities and constraints appear when climate changes, leading to adaptation in the use of land resources (Jeltsch et al. 2011; Bradley et al. 2012). Moreover, models foresee that future climate change will result northward shifts of maize area in the United States, or rice area in China (Tubiello et al. 2002; Xiong et al. 2009). Consequently, effective and efficient conservation policy has to be based on the direct climate effect on species and the indirect effects induced by human adaptations, strategies and public policies (Hannah et al. 2002; Berrang-Ford et al. 2011; Johnston et al. 2013). This paper presents an integrated bio-economic framework to explore the interactions among climate change, land use and biodiversity. This framework is structured in three modeling blocks: Species Distribution Models (SDM) of bird abundances and distributions, econometric models of LUC and Ricardian models of returns from land in response to climate change. This integrated structure is then used to simulate climate change effects on future land uses and bird distributions from the present to 2053 based on climate and economic projections, and an example of spatially uniform conservation policy.

Firstly, in the SDM, the abundances of common bird species are related to local environmental conditions (Furness and Greenwood 1993; Gregory et al. 2005; Renwick et al. 2012). SDMs assume that habitat and climate requirements can be deduced from current distributions, and that future abundance and distributions can then be extrapolated using projections of future climate and habitat changes (Peterson et al. 2011). SDM for this study are developed using avian data from the French Breeding Bird Survey (FBBS), a standardized monitoring scheme in which skilled volunteer ornithologists identify breeding birds by song or visual contact every Spring (Jiguet et al. 2012). Observations indicate that bird populations are decreasing for pasture habitat specialists (Devictor et al. 2008) and are shifting up in altitude and towards the north as a result of recent climate warming (Jiguet et al. 2010). Secondly, the econometric LUC model fits the private land use decisions as functions of economic returns (Lubowski et al. 2008; Nelson et al. 2008; Radeloff et al. 2012). This model is based on a analysis of observed land use data from the TERUTI land use survey (France, 1993–2003). TERUTI data have already been used for econometric LUC models but not for the whole France at the fine level of spatial resolution used in this study (Chakir and Parent 2009; Chakir and Le Gallo

2013). The econometric model is then used in a step-by-step scenario analysis to isolate and illustrate the impacts of the individual drivers of bird species abundance and distribution. Finally, the Ricardian model uses observed co-variations of land prices and climate to infer the potential future consequences of climate change on the economic returns from land (Mendelsohn et al. 1994; Mendelsohn and Dinar 2009). This approach is developed at the scale of France on the basis of land prices from the statistical services of French Ministry of Agriculture and regionalized climate data (Déqué 2007; Boé et al. 2009).

This paper addresses three main questions:

(i) What is the effect of climate change on common bird abundances, assuming either constant or economically driven land use changes?
(ii) Does climate-induced land use change mitigate or amplify the direct effects of climate change on common birds abundances?
(iii) What is the effect on LUC and common bird abundances of a uniform conservation payment to landowners irder to promote pastures?

First, our model projects a significant negative impact of climate change on bird abundances by mid-century. This effect is strong relative to the effect of projected land use change. Locally, climate change is projected to result in a greater elevation shift than northern shift in the distribution of birds. Second, climate-induced LUC is foreseen to amplify the negative direct effects of climate change on birds. This is not the case everywhere, with some locations, particularly in southern France that are projected to benefit from climate-induced LUC. Third, we find that spatially uniform payments of 200 euro.ha^{-1} to promote pastures only slightly counteract the negative effects of climate change. We foresee that these relatively high payments will have a positive effect in relatively few locations and only on the least vulnerable species.

2 Models

2.1 Species Distribution Models

Bird abundance and distributions are modeled with an SDM that accounts for the potential impact of climate and habitat (Pearson and Dawson 2003). For a general description of the method, we note μ_{tqs} the abundance of species s in the FBBS sampling square q at the time t and we assume the following relationship between the outcome and its predictors:

$$\log(\mu_{qst}) = \lambda_s(\mathbf{c}_{qt}, \mathbf{h}_{qt}, \mathbf{x}_q, \mathbf{z}_q) + \delta_s \cdot t, \tag{1}$$

where the $\lambda_s(\cdot)$, $s = 1, \ldots, S$ are spline-based smoothing functions with an endogenous structure as is common for Generalized Additive Models (GAM, Hastie and Tibshirani 1990; Wood 2006). The smoothing functions have to be estimated, as the scalars δ_s that capture the linear growth 2003–2009 for each species s (see Online Resources OR1.1 for more details about avian data). $\mathbf{c}_{qt}$ stands for the two principal axes at location q and time t of a Principal Component Analysis of the climatic variables matrix. The Figure ORF1 shows the relationships between the climate variables and these 2 principal axes, which account for 87% of the total variance. $\mathbf{h}_{qt}$ is the vector of habitat variables including a fragmentation index, $\mathbf{x}_q$ represents a vector of topographic variables (also from a PCA of topographic variables reported in ORF1) while $\mathbf{z}_q$ is the spatial location of the center of gravity of each FBBS square. Including these spatial coordinates in the smoothed functions allows us to separate the unobserved contextual effects (i.e., inter-species competition, spillovers from anthropogenic perturbations) from the direct topographic, climatic and habitat effects. Because bird abundances are over-dispersed positive integers, they are modeled as a distribution from the negative binomial family. The function `gam()` from the `R` package `mgcv 1.7` was used to estimate such models (Wood 2006). Because the impacts of climate change on species distributions have been shown to vary depending on choice of modeling technique (Buisson et al. 2010 and Garcia et al. 2012) and of spatial structure (Dormann et al. 2007), we have estimated other SDMs based on alternative assumptions. We also fitted negative binomial mixed models without including geographical coordinates (with the `R` package `glmmADMB`, see ORT5) and zero-inflated hurdle models with and without geographical coordinates (with the package `pscl`, see ORT6). From the time dimension, Figure ORF10 presents the predictions from 3 scenarios relying on 4 different SDMs. From the space dimension, the 15 Pearson correlation coefficients between the projections are comprise between 0.50 and 0.98, with more than the half greater than 0.8 (Figure ORF11). Including geographical coordinates increases the goodness-of-fit but have a relative limited impact on abundance variations within scenarios, we focus only on the results from the negative binomial GAMs here for the sake of clarity.

2.2 Econometric model of Land Use Changes

We have reduced land use types to five ($L = 5$) mutually exclusive categories: annual crops, perennial crops, pastures, forests and urban areas (see OR1.2). Landowners are assumed to choose LUC in order to maximize their utility[1] and these choices are assumed to be independent for each parcel. With this latter simplifying assumption, each parcel is associated with a distinct decision process. In particular, a stylized landowner i chooses the land use type ℓ^*_{it} on a parcel if this provides the highest utility over all possible uses:

$$\ell^*_{it} = \arg\max_{\ell} \{u_{i\ell t}\}. \tag{2}$$

This formulation for utility is forward-looking and accounts for the possibility of multi-year land use such as perennial crops, forest or urban. Utility is typically assumed to be the expected one-period net returns that are the outcome of a dynamic optimization problem (Plantinga 1996; Lubowski et al. 2008). We exploit this result here by assuming a parametric but nevertheless flexible structure between the expected returns and utility. At t, for each land use ($\forall \ell = 1, \ldots, L$) and for each sampled plot ($\forall i = 1, \ldots, I$), we assume:

$$u_{i\ell t} = \alpha_\ell + \mathbf{r}_{it}\boldsymbol{\beta}_{1\ell} + \mathbf{c}_{it}\boldsymbol{\beta}_{2\ell} + \mathbf{x}_i\boldsymbol{\beta}_{3\ell} + \mathbf{r}_{it}(\mathbf{c}_{it} + \mathbf{x}_i)\boldsymbol{\beta}_{4\ell} + \mathbf{h}_{it-1}\boldsymbol{\eta}_\ell + \epsilon_{i\ell t}. \tag{3}$$

[1] Rationality is not a necessary condition, as Train 2009 (Chap.2, p.14) explains: "The derivation assures that the model is consistent with utility maximization; it does not preclude the model from being consistent with other forms of behavior. The models can also be seen as simply describing the relation of explanatory variables to the outcome of a choice, without reference to exactly how the choice is made."

Where $\mathbf{r}_{it}$ is the vector of net returns in t for each of the possible land uses on parcel i. These rent variables are only available at the scale of the Small Agricultural Region (SAR, see ORT4 for a synthesis of the spatial units used to match the data). As such, they are crossed with climate $\mathbf{c}_{it}$ and constant biophysical variables $\mathbf{x}_i$ (elevation, slope and land quality) to allow parcel-level deviations from the aggregate effects. Conversion costs between uses are taken into account by including $L-1$ dummy variables representing the previous land use of a parcel i: $\mathbf{h}_{it-1}$. So, the vector $\boldsymbol{\eta}_\ell$ estimates the costs to change to land use ℓ. Each vector of coefficients to estimate $[\alpha_\ell; \boldsymbol{\beta}_{\cdot\ell}; \boldsymbol{\eta}_\ell]$ is unique for each land use category ℓ. This means that expected economic returns, climate, biophysical variables and conversion costs could have heterogeneous effects on the utility, depending on the land use.

Because all the sources of landowner's utility cannot be observed, an error term $\epsilon_{i\ell t}$ is included in (3). McFadden (1974) identifies three criteria for using a multinomial logit model: independence, homoscedasticity and extreme value distribution (i.e., Gumbel). Assuming these criteria are met, one can show that the probabilities have simple closed forms, which correspond to the logit transformation of the deterministic part of the utility function ($\bar{u}_{i\ell t} \equiv u_{i\ell t} - \epsilon_{i\ell t}$). The probability that a parcel i is in use ℓ at the period t is:

$$p_{i\ell t} = \frac{\exp(\bar{u}_{i\ell t})}{\sum_k \exp(\bar{u}_{ikt})} = f_\ell\big(\mathbf{r}_{it}, \mathbf{c}_{it}, \mathbf{x}_i, \mathbf{h}_{it-1}\big). \tag{4}$$

The estimation was performed using `nnet 7.3` on `R`. The unobserved factors are assumed to be uncorrelated over alternatives and periods, as well as having a constant variance. These assumptions, used to provide a convenient form for the choice probability, were found to be not restrictive (homoscedasticity cannot be rejected by a score test, p-value= 0.283). Moreover, these hypotheses are associated with the classical restriction of Independence of Irrelevant Alternatives (IIA) for which Hausman-McFadden specification tests are performed, with mixed evidence. The independence is not rejected for three uses: pasture, perennial crop and urban (p-values are respectively 0.001, 0.005 and 0.036) but rejected for annual crop and forest at 5%. In the land use econometric literature, use of nested multinomial logit is found not to change the results (Lubowski et al. 2008).

2.3 Models of economic returns

In the Ricardian model, the price of land is used to compute the expected net returns from land uses. Land is considered as a classical fixed asset, implying that its price $v_{\ell t}$ at time t for the use ℓ is equal to the net present value of all expected future rents for land use ℓ. Assuming flat interest rates $\tau_t = \tau$ and flat rates of capital gains $g_t = g$, this reads as follows:

$$v_{\ell t} = \sum_{s=1}^{\infty} \frac{\mathbb{E}_t(r_{\ell t+1})(1+g)^s}{(1+\tau)^s} = \frac{\mathbb{E}_t(r_{\ell t+1})}{(\tau - g)}. \tag{5}$$

$\mathbb{E}_t$ is the expectation operator at t is noted. Thus, the expected return of a land plot on the basis of its observed price, $r_{\ell t} = (\tau - g) \cdot v_{\ell t}$, can be calculated knowing the interest rate and the rate of capital gains $(\tau - g)$. This result depends on the assumption of well-functioning markets (i.e., competitive and balanced) and so has to be considered as a theoretically-consistent first approximation.

We use a Ricardian equation to model the effect of climate change on land prices $v_{\ell t}$ or, equivalently, on the expected net returns $r_{\ell t}$ of annual crop, pasture, perennial crop and forest. The Ricardian equation relates the economic returns of land to climate, other biophysical variables and geographical coordinates as follows:

$$\log(r_{i\ell t}) = y_\ell\big(\mathbf{c}_{it}, \mathbf{x}_i, \mathbf{z}_i\big) + \gamma_\ell \cdot t. \tag{6}$$

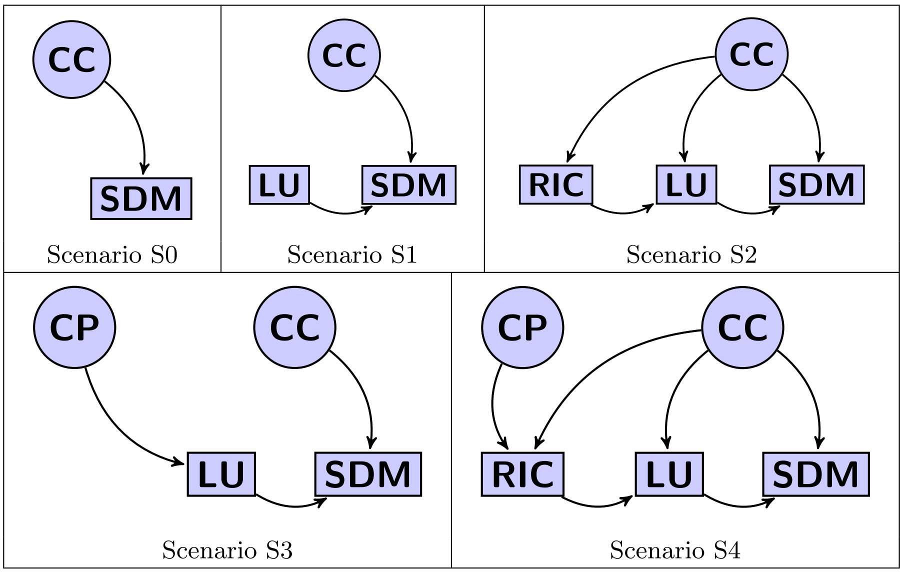
$y_\ell(\cdot)$ is a spline-based smooth function with endogenous structure which depends on the type of land use ℓ. Thus, these functions and the γ_ℓ are estimated on the cross-sectional variations between Small Agricultural Regions and the time series 1993–2003 (see OR1 for more details). The Ricardian equations are estimated separately for annual crop, pasture, perennial crop and forest using GAM with a distribution from the Gaussian family and a natural logarithm link. For the dynamics of the urban returns, we use the spatialized projections of population growth by the French demographic institute. Because these projections are available at the *département* scale (*départements* are a French administrative division that range in size from ca. 600 to 10,550 km^2, see Table OR4), we have downscaled them by assuming that each municipality keeps a constant proportion of the aggregate values.

2.4 Scenarios of the interactions between land use, climate and biodiversity

We explore several scenarios that differ in the dynamics of the deterministic part of landowners' utilities of (4). The estimated logit regression function $\widehat{f}_\ell$ and the biophysical variables $\mathbf{x}_i$ are assumed to stay constant in time and are identical in all scenarios. But, depending on the scenario, the economic returns $\mathbf{r}_{it}$ and/or the climate variables $\mathbf{c}_{it}$ are allowed to change. We consider five scenarios that are presented in Figure 1. The scenarios contain two to five of the following components: climate change (CC), species distribution models (SDM), land use (LU), Ricardian model of returns (RIC) and conservation payments (CP). The objective of this step-by-step analysis is to isolate and illustrate the impacts of the individual drivers of bird species abundance and distribution.

The scenarios were carried out as follows. Once the LUC model is estimated based on past land use ($\mathbf{h}_{it-1}$), environmental and economic variables ($\mathbf{c}_{it}$, $\mathbf{x}_i$, and $\mathbf{r}_{it}$), the direct predictions consist, for each parcel of land i, in a fitted probability vector $\widehat{\mathbf{p}}_{it}$ of being in each land use at t. Because the model is estimated on LUC 1993–2003, we consider 1993 as the period $t = 0$ and 2003 as the period $t = 1$: our model is recursive with decennial steps. Since each TERUTI parcel represents 100 ha, the predicted probabilities can be converted into spatially-explicit projected LUC. As an example, consider a parcel i which counts for 100 ha of annual crop in period 0 and has a predicted probability vector for period 1 of $\widehat{\mathbf{p}}_{i1} = (0.8, 0.15, 0.03, 0.01, 0.01)$. This means that 80 ha are predicted to not change their use, 15 ha to be converted to pasture, 3 ha to perennial crop, 1 ha to forest and 1 ha to urban. Land use at $t = 1$ (2003) is common to all scenarios and, for S0, it is the same at $t = 2$ (2013), $t = 3$ (2023), $t = 4$ (2033), $t = 5$ (2043) and $t = 6$ (2053).

Fig. 1: **Inclusion of relationships between climate change (CC), Ricardian models of returns from land (RIC), land use (LU), conservation payments (CP) and species distribution models (SDM) in different scenarios.** Simulations of bird populations by SDM pursue the observed 2001–2009 trends and integrate climate change in all scenarios. In scenario S0, land use is constant. In scenario S1, the model of LUC is used to extrapolate the temporal trends to obtain a kind of business-as-usual scenario. In scenario S2, the effects of climate change on the returns from land and, consequently, on LUC are taken into account. Scenario S3 and S4 are respectively equivalent to S1 and S2 with a conservation policy providing uniform payments for pastures



For the other scenarios, LUC simulation for $t = 2$ is performed by substituting the dynamics of certain exogenous variables in regression equations. For S1, only t is implemented in the Ricardian equation (6) to obtain the economic returns $\widehat{\mathbf{r}}_{i2}^{S1}$ that are then used in the logistic equations (4). For S2, climate variables $\mathbf{c}_{it}$ are implemented in the Ricardian equations (6) and in the logistic equations (4). For both scenarios, we predict a probability matrix of land use in $t = 2$ conditionally on previous land use: $\widehat{\mathbf{h}}_{i2} = \widehat{\mathbf{p}}_{i2}(\mathbf{h}_{i1})$. Calculations for the first time step in the simulation are facilitated by the knowledge of the previous use for each surveyed parcels in the 2003 TERUTI survey: $\mathbf{h}_{i1}$. After $t = 2$, simulation of LUC changes: instead of a single previous use for each plot, there is a vector of probabilities: $\widehat{\mathbf{h}}_{i2}$. For $t > 2$, LUC is therefore computed in a different manner. For each potential use ℓ on a plot i, the simulated land use is:

$$\widehat{h}_{i\ell t} = \widehat{\mathbf{p}}_{it}(\mathbf{h}_{it-1} = \mathbf{1}_\ell) \cdot \widehat{\mathbf{h}}_{it-1}, \tag{7}$$

where $\mathbf{1}_\ell$ is a $1 \times L$ vector with the ℓ-component equals 1 and the others are equal to zero. In other words, variables describing land use are dummies to predict transition probabilities but they are values inside the unit interval to simulate land use. Because LUC transition probabilities are functions of expected returns of each land use, the inclusion of an incentive-based policy is straightforward. This possibility is illustrated here through the study of a spatially-uniform payment of 200 euro.ha^{-1} for pastures.[2] This policy consists, for $t > 1$, in increasing the rents for pastures ($\ell = 3$) used to fit transition probabilities:

$$\widehat{r}_{i3t}^{S3} = \widehat{r}_{i3t}^{S1} + 200 \qquad \text{and} \qquad \widehat{r}_{i3t}^{S4} = \widehat{r}_{i3t}^{S2} + 200. \tag{8}$$

For the others uses, the respective economic returns of S3 and S4 are the same as S1 and S2. To test the dependency of our results on the payment amounts, we tested two other levels (100 euro.ha^{-1} and 300 euro.ha^{-1}). These analyses indicate that the overall increase of pastures depends on payment amounts. However, the spatial patterns resulting from varying the payment amounts are very similar.

For all scenarios, LUC are used in the SDM to predict bird abundances at the same spatial and temporal scales. In this final stage, the LUC effects are coupled with the direct effect of climate change on bird distribution. To evaluate the overall effects on birds we use an abundance-based index, the geometric mean of abundances normalized by the abundances of the year 2003 (t =1):

$$BI_{mt} = \prod_{s \in S} \left(\frac{\widehat{\mu}_{ms}(t)}{\mu_{ms}(1)} \right)^{1/|S|} \tag{9}$$

where m is the geographical scale at which the index is computed, either at the national scale or the 12×12 km TERUTI grid to produce maps (see ORT4). Applied to farmland specialists species, this index is the well-used European Farmland Bird Index but we also use it for birds species as a whole and for other habitat specializations: generalist, forest and urban. We use the formula from Gregory et al. (2005) to compute the standard errors.

3 Results

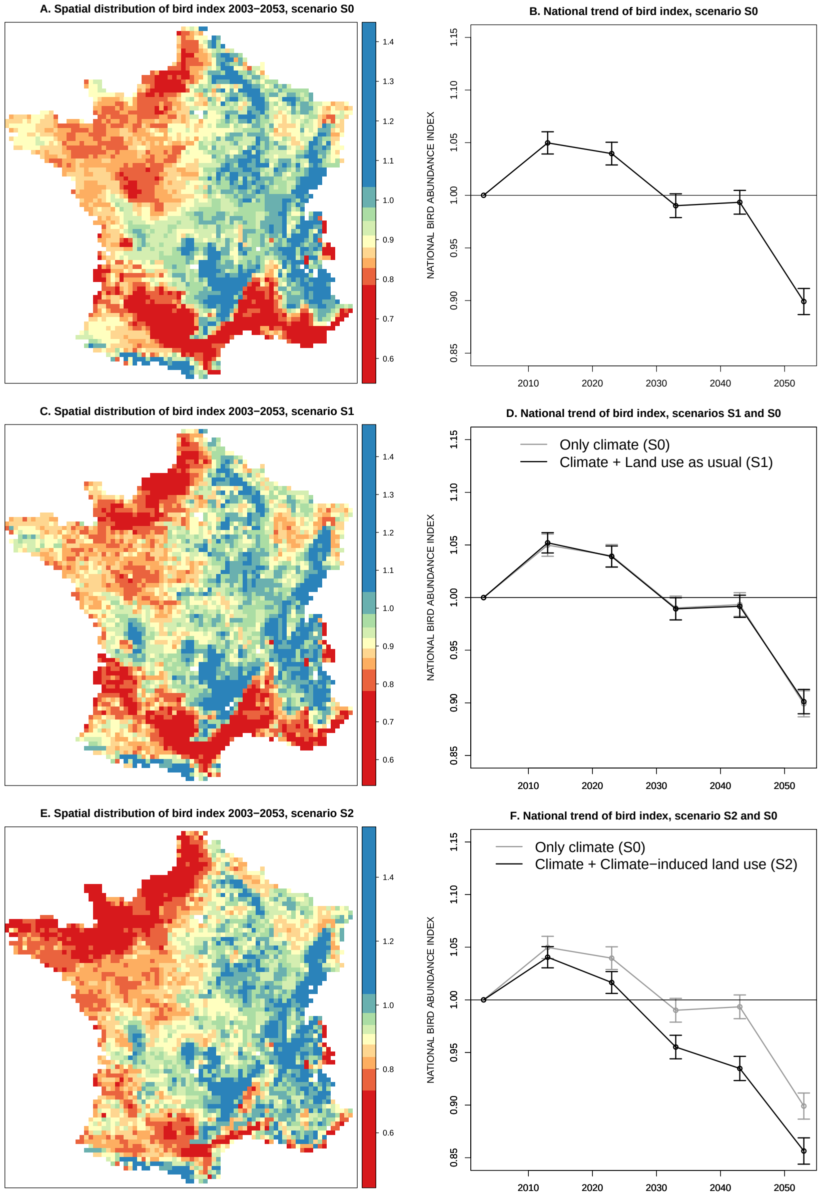
3.1 Climate change impacts on birds without LUC (scenario S0)

The first scenario focuses on projecting the effects of climate change on bird populations assuming that land use does not change over time. Under the IPCC SRES A1B regionalized climate projection, the annual temperature of France is projected to increase by + 2.0°C ± 0.2 s.d. up to 2053. The annual cumulative precipitation is projected to decrease by − 13.4 mm ± 6.3 s.d., the relative humidity to decrease by − 1.7 % ± 1.2 s.d. and the solar radiation to increase by + 17.1 J ± 14.4 s.d. As displayed in the Panel B of Figure 2 from a national viewpoint, the effect of climate change on the aggregate bird index is first positive (+ 5% up to 2023), not significant for 2033–2043 and strongly negative from 2043 onward (− 10% at 2053).

The spatial precision of the projected climate (8 × 8 km) allows us to model more precisely than usual the geographical shifts in bird distributions. As shown by

[2] In the European Common Agricultural Policy, a significant amount of agri-environmental schemes are payments depending on land use. Since 2007, the French government has taken over an acreage payment of 76 euros by ha and by year for pastures. Our stylized payment is close to a rather ambitious version of this, doubling over the payment.

Fig. 2: **The effects of climate and land use changes on the index of bird abundances for the scenarios without conservation: S0, S1 and S2**



the panel A of Figure 2, the Mediterranean coast at the southeast and the center of the southwest are two regions of important decline in bird populations. Detrimental effects, albeit less strong, appear in the northwest of France. In contrast, bird populations in the continental part of the country – the east and center – have positive growth rates (up to + 40%). These dynamics of bird populations are best explained by average 2003 temperatures and average elevation (respective Pearson's correlations of − 0.51 and + 0.42, both p-values <0.001).

In this scenario, land use is constant but plays an important role in determining the dynamics of bird populations. The Figure ORF2 shows that the direct effect of climate on bird species depends on their land use preference. Climate change for the last period of analysis, 2053, has a significant negative impact on generalist species (about − 10 index points), forest specialists (about − 30 index points) and urban specialists (about − 2.5 index points). By contrast, the model predicts that the abundances of farmland specialists increase by about + 10% over this period. The mechanisms driving this effect are that climate-induced shifts in bird species distributions are toward areas of more favorable land uses for farmland specialists. Pastures are generally at higher elevation than annual crops and climate change drives bird distributions towards these higher elevations. The Figure ORF3 provides the individual rates of variation for each bird species abundances 2003–2053. Climate change significantly affects the large majority of species (the variations of only 2 species are not significant while 21 species increase and 39 decrease).

3.2 Climate change impacts on birds with extrapolated trends of LUC (scenario S1)

The first scenario including LUC was simulated by extrapolating the 1993–2003 trends of economic returns to future LUC. This scenario accounts for climate change impacts on birds as in S0, but not on land use. Panel (a) of Table 1 presents the national land allocation 2003–2053 with decennial steps for this scenario. This simulation projects an extension of recent trends: an increase of annual crop, forest and urban area (respectively + 3.17%, + 9.11% and + 33.4%) and a decrease in pasture and perennial crop area (both of − 17.7%). The urbanization of land is the largest trend in relative terms. The dynamics of annual crops is less monotone with a small loss for 2003–2013, an increase in the period 2013–2033 and stagnation between 2033–2053.

The effect of LUC on birds in the scenario S1 is globally neutral: the differences with S0 are small and not significant (see Panel D of Figure 2). In S1, the aggregate bird population index is influenced almost exclusively by climate change. Spatially, the general pattern of S0 is maintained but there is some mitigation of impacts in certain parts of the south of France and an amplification at the northwest (see Panel C of Figure 2). To disentangle the effects of S1 LUC from the climate effects, the Figures ORF4 and ORF5 present the net effects of S1 LUC with constant climate. It appears that S1 LUC effects are much smoother and more homogeneous between species with the same habitat preferences (compared to the effects plotted in Figure ORF2). They are positive and significant for urban specialists and generalists, not significant for forest specialists and negative and significant for farmland specialists. From individual species point of view, populations significantly grow for 15 species as a result of S1 LUC, 10 decrease significantly and 37 do not exhibit significant change.

Table 1: **National acreages of land uses in thousand km^2 and associated growth rates for scenarios S1, S2, S3 and S4** ANCR areas for annual crops, FORE for forests, PECR for perennial crops, PAST for pastures and URBA for urban. The two last rows, named $\Delta(\%)$, present the growth rates 2003–2053

Extrapolating current trends of land use changes										
	(a) S1: Without conservation					(b) S3: With conservation				
YEAR	PECR	ANCR	PAST	FORE	URBA	PECR	ANCR	PAST	FORE	URBA
2003	141.3	1,573.5	1,529.8	1,580.4	315.7	141.3	1,573.5	1,529.8	1,580.4	315.7
2013	135.1	1,571.7	1,472.6	1,610.1	351.3	130.3	1,397.2	1,718.2	1,561.3	333.8
2023	128.2	1,606.6	1,390.0	1,643.9	371.9	119.9	1,334.1	1,789.1	1,555.3	342.4
2033	123.2	1,621.5	1,332.4	1,673.6	389.9	112.4	1,292.8	1,832.7	1,551.2	351.6
2043	119.3	1,625.4	1,290.2	1,700.1	405.6	106.8	1,265.3	1,859.5	1,548.2	361.0
2053	116.2	1,623.0	1,258.1	1,724.2	419.3	102.6	1,246.4	1,875.7	1,546.0	370.1
$\Delta(\%)$	– 17.7	+ 3.17	– 17.7	+ 9.11	+ 33.4	– 27.6	– 20.79	+ 22.6	– 2.15	+ 17.5
Climate-induced land use changes										
	(c) S2: Without conservation					(d) S4: With conservation				
YEAR	PECR	ANCR	PAST	FORE	URBA	PECR	ANCR	PAST	FORE	URBA
2003	141.3	1,573.5	1,529.8	1,580.4	315.7	141.3	1,573.5	1,529.8	1,580.4	315.7
2013	185.8	1,687.0	1,327.5	1,593.6	346.9	184.1	1,611.6	1,436.0	1,573.8	325.2
2023	181.4	1,833.4	1,146.0	1,614.0	365.9	176.2	1,579.8	1,519.7	1,541.6	333.4
2033	198.5	1,935.6	973.9	1,630.8	401.8	183.2	1,635.8	1,477.2	1,514.8	339.7
2043	217.4	2,096.6	754.8	1,625.9	446.1	193.7	1,836.2	1,278.5	1,486.4	345.9
2053	306.6	2,038.6	680.8	1,607.5	507.3	259.7	1,827.1	1,233.5	1,431.3	389.1
$\Delta(\%)$	+ 177	+ 27.15	– 55.5	+ 1.71	+ 60.1	+ 83.7	+ 16.15	– 19.36	– 9.43	+ 23.5

3.3 Climate change impacts on birds with climate-induced LUC (scenario S2)

The integration of the effects of climate on the returns of land by the Ricardian models is presented in Table 2. Up to 2053, the returns are predicted to increase for annual crops (md.= + 117%), pastures (md.= + 74%) and perennial crops (md.= + 13%). The median increase of the density of population is + 28% but the median rate of variation for returns from forest is negative: – 13%. Climate change is also found to flatten the distribution of returns (i.e., it increases standard errors) in terms of economic returns for annual crops, pastures and urban.

Panel (c) of Table 1 presents the consequences of these variations of economic returns on LUC. Except for perennial crops, climate-induced LUC are in the same directions compared to the scenario S1: annual crops, forests and urban increase and pastures decrease. The effect of climate change on perennial crops is strong (+ 177%) and is mainly explained by the high growth rate at the top of the distribution of returns. As a consequence, this growth regards only a few locations already specialized in perennial crops (southeast in particular). The important decrease of pastures (– 55%) is mainly explained by the expansion of annual crops and urban areas. The growth rate of urbanization in S2 is twice the rate of S1 although the same scenario in terms of demographic growth was used. This indicates an increase of low-density exurban housing which was already been shown to be an important threat to breeding birds (Jongsomjit et al. 2013).

The Panel (f) of Figure 2 shows that climate-induced LUC amplifies the negative effect of climate change on the aggregate bird index. With climate-induced LUC,

Table 2: **The Ricardian effects of climate change on the economic returns from land: amounts in current euros and in variations** The mean values of returns are in current euros/ha for the first 4 rows and hab/km^2 for the last. SE is for standard errors, variations are expressed in %. ANCR counts for annual crops, FORE for forests, PECR for perennial crops, PAST for pastures and URBA for urban

	2003		**2053**		**Variations 2003–2053**				
Land Use	Mean	SE	Mean	SE	Min	Q1	Q2	Q3	Max
ANCR	265.4	92.27	587.7	346.2	– 100.0	+ 72.05	+ 116.8	+ 159.4	+ 323.5
PAST	113.9	73.35	191.7	103.8	– 24.10	+ 52.62	+ 73.81	+ 98.21	+ 341.7
PECR	177.3	730.1	185.6	699.4	– 75.18	+ 4.474	+ 13.35	+ 19.01	+ 196.0
FORE	80.90	60.07	69.92	53.31	– 44.76	– 16.25	– 13.18	– 8.742	+ 45.36
URBA	81.98	291.8	103.0	386.8	– 29.10	+ 13.99	+ 28.31	+ 46.81	+ 109.4

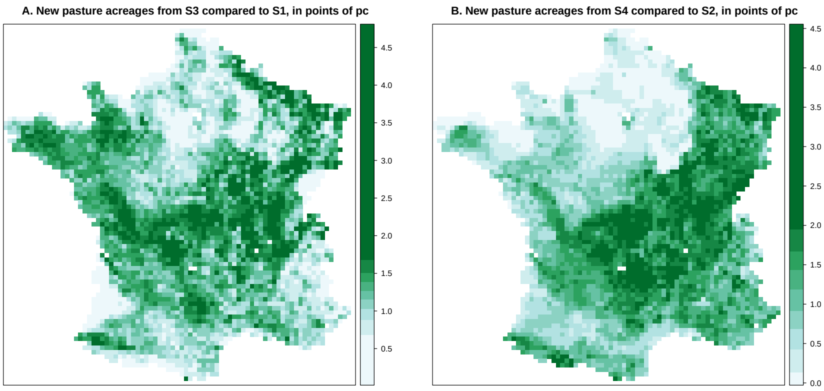
the national bird index shows a decrease of 14% of abundances in 2053, compared to 10% in the case of constant land use S0. Panel E of Figure 2 indicates a strong spatial redistribution of the loss in terms of abundances. An important part of the most detrimental effects of climate change in the southeast are mitigated by climate-induced LUC. In contrast, an amplification of the effect of climate change appears in the northeast. Climate change induces a northern shift of annual crops and an increase of urban areas and perennial crops in the south which explain these results.

The effects of S2 LUC on bird species grouped by habitat preference and for each species separately are shown in Figures ORF6 and ORF7, for bird species grouped by habitat preference and for each species separately. In this scenario, only urban specialists benefit from climate-induced LUC: + 10.5%. Other groups undergo a significant decrease in abundance for 2053: respectively – 5%, – 7.5% and – 8.5% for generalist, farmland and forest specialists. The effects of S2 LUC, not including direct climate impacts on birds, are negative and significant for 41 species and positive for only 12 species. The latter are all urban specialists except the Eurasian skylark (*Alauda arvensis*) that is a farmland specialist.

3.4 Climate change impacts on birds and land use with payments for pastures (scenarios S3 and S4)

An annual, spatially-uniform, payment of 200 euro.ha^{-1} was coupled with scenario S1 to produce S3 (see Figure 1). In this scenario, the payments for pasture are sufficient to reverse the predicted decline of pasture over the next few decades, see the Panel (b) of Table 1. This payment results in a projected net increase of + 22.6% of pasture area in the period 2003–2053. Urbanization still occurs but in a more moderate way relative to S1 (+ 17.5%). Pastures induced by such a policy (new pastures but also pastures that are not converted) replace principally annual and perennial crops in the scenario S1. This scenario projects a decrease forest share, but the loss is small, – 2.15%. The spatial distribution of these payment-induced pastures are presented in the panel A of Figure 3. Areas of annual crop specialization (around *Paris* at the northern center) and of forest specialization (extremes southwest and southeast) are not heavily affected by the policy which are well spread over locations.

Fig. 3: The net effects of the payments for pastures of 200 euros/ha on pastures in scenarios S3 and S4, relative to S1 and S2 respectively.

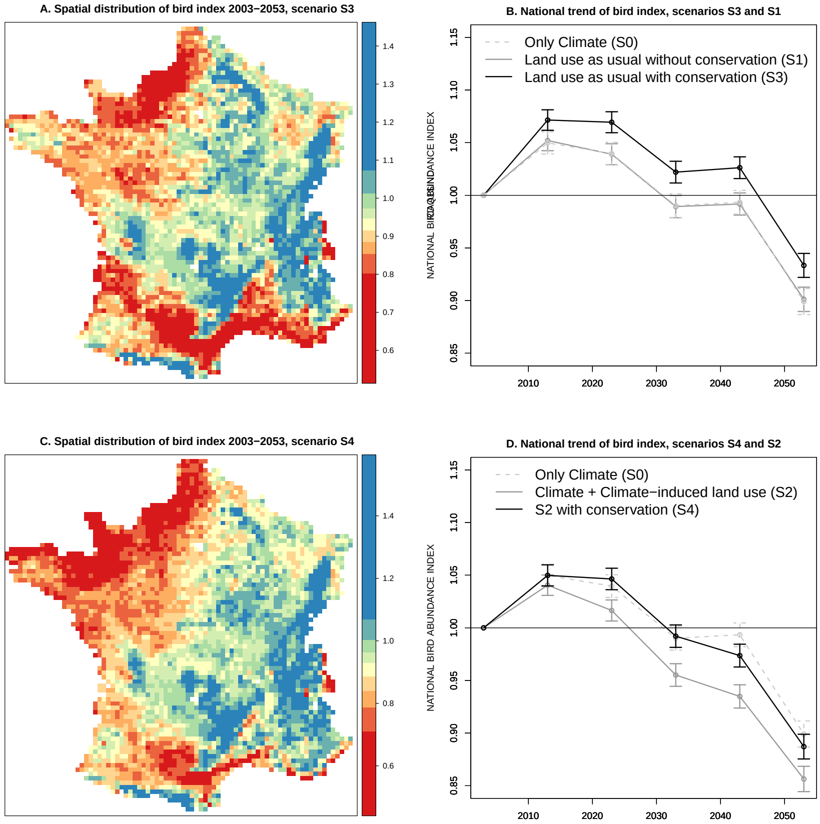


However, when climate change impacts on LUC are accounted for (i.e., when pasture payments are included in S2 to obtain S4), the payments for pasture do no longer entail a net increase in pastures, see the Panel (d) of Table 1. Nevertheless, the predicted loss is highly restricted relatively to S2, and the 2053 area of pastures with conservation policy (S4) is nearly than twice that without conservation (S2). The payments for pasture in this scenario are still accompanied by an increase of annual crops because, as noted above, crops returns increase both by the extrapolation of trends and the benefit from climate change by the Ricardian effect. Payments for pastures lower the rate of increase in urbanization[3] even though this land conversion remains high (+ 23.5%). This scenario S4 leads to the highest loss of forest area (− 9.4%) due to decreasing returns of forests induced by climate change and competition with pastures arising from payments.

For both policy scenarios S3 and S4, the payments for pasture are projected to significantly increase the national bird population index but are not sufficient to counteract the negative effects of climate change (Panels B and D of Figure 4). The national trend in bird abundances is always primarily shaped by climate change (i.e., first a small increase then a bigger decrease) even when effects of payments for pastures are statistically significant. For S3, the negative effects of climate are delayed to 2045 instead of occurring by 2030 for S1. For S4, the policy of payments for pastures results in 2053 bird abundances close to S0 (about − 10%), indicating

[3] The high proportions of change (− 1/2 both for S3 and S4 relatively to S1 and S2) are somewhat surprising but have to be put in perspective in terms of acreages. They represent respectively 50,000 and 110,000 ha where the differences for pastures are around 550,000 ha between scenarios. The differences in urban areas are nevertheless sufficiently marked to highlight a competition for space between urban and pastures, and between urban and conservation. The low opportunity cost of pasture is probably the reason for this result.

Fig. 4: The effects of climate, land use changes and conservation policy on the index of birds abundances for scenarios S3 and S4.



that it partially counteracts the negative effects of climate-induced LUC. It is also interesting that the effects of the 200 euros.ha^{-1} payment on the differences between S3 and S1 and between S4 and S2 are relatively similar: about + 2.5 points of the national bird index.

Figures ORF8 and ORF9 present the net effects of both scenarios with payments for pastures at the level of bird species. For S3, the effects of payments are generally positive. They involve detrimental effects only for 10 species across all habitat preferences. The biggest improvements due to conservation regard farmland specialists: Whinchat (*Saxicola rubetra*), Hoopoe (*Upupa epops*), European Stonechat (*Saxicola rubicola*) and Red-backed Shrike (*Lanius collurio*). For S4, conservation negatively affects 20 species from all habitat preferences. But strong positive effects are found for certain species, in particular species that are strongly declining in S2 (see of the bottom of the Figure ORF9). This mitigation effect from habitat-based conservation is insufficient to counteract the patterns induced by climate change.

4 Discussion and conclusion

This study compares 5 different model-based scenarios of land use and climate impacts on an index of bird abundance for France over the period 2013–2053, driven by a downscaled IPCC A1B climate projection. The scenarios differ in the way they account for land use impacts and in the role played by economic returns, public policies, and climate on LUC.

A first result of our scenario analysis is that the bird community dynamics are projected to be more heavily impacted by climate change than by LUC in France. This contradicts global studies suggesting that land use will dominate biodiversity dynamics over the next few decades as compared to climate change (Pereira et al. 2010) but in accordance with other recent local scale evidence (Martin et al. 2013). There are several possible explanations for this. Firstly, the SDMs predict that bird species are generally more sensitive to climate variables than habitat or topographic variables. Second, the projected land use changes for France over the next four decades are relatively modest, while projected climate change is relatively large in the climate scenario that we used. However, the robustness of these results need to be further evaluated for several reasons. In this study, we used bird abundance data only from France meaning that some climatic and habitat niches of birds are truncated, potentially leading to an overestimation of the risk of local decline or extinction (Barbet-Massin et al. 2010). In this respect, the refinement and reinforcement of models by expanding the dataset, in particular the extension to the European scale, could be valuable (Barbet-Massin et al. 2011). Moreover, using common birds abundance as a proxy for biodiversity has important limits (Renwick et al. 2012) but birds are a highly sensitive indicator of climate change and habitat due to their rapid population and range responses to both drivers (Jiguet et al. 2010; Renwick et al. 2012).

A second contribution of the paper is to provide an econometric model of LUC and to account for the economic effects of returns from land and market-based policies on private decisions (Lewis et al. 2011). In particular, changing the monetary returns from land is projected to be sufficient to induce significant differences in terms of LUC. Although the LUC models in this paper provide important insights into the factors mediating future land use, they could be improved in several ways. One possible improvement is to explicitly take into account spatial autocorrelation of the outcome variables (Chakir and Parent 2009; Chakir and Le Gallo 2013). Another improvement relates to the legitimate concern that the correlations underlying the relationships in the econometric equations may change over the long-run, and that this problem may be even more acute for the Ricardian equation. The robustness of our results in terms of climate change impacts also need to be further evaluated because we have used a single climate projection. We have used a climate change scenario with a mean annual temperature increase that is close to the multi-model IPCC AR4 projections for A1B emissions scenarios; however, the scenario we used is one of the driest AR4 climate projection for France (Cheaib et al. 2012). However, accounting for broader range of projected climate changes would substantially increase uncertainty in projections of bird population change and LUC compared to those explored here (Katz et al. 2013). In addition, climate impacts are highly dependent on the spatial scale of climate projections, especially in mountainous areas (Franklin et al. 2013).

Thirdly, our results also suggest that there are large species-specific differences in the response of birds to climate change (Jiguet et al. 2010). For conservation policies, this stresses the complex, coupled responses of biodiversity and land use to climate change and policies affecting LUC (Bradley et al. 2012; Johnston et al. 2013). By contrast, the conservation policies must remain simple for the sake of clarity with respect to stakeholders, especially landowners, and for avoiding prohibitive implementation and monitoring costs (Wintle et al. 2011). The incentive-based policies with a fixed-amount payment for pasture at the national scale is a first step towards such a balance in the vein of Lewis et al. (2011) and Mouysset et al. (2011). Moreover, we found that such payments can help counteract the impacts of land-use change, but fully counteracting the negative effects of climate change on bird populations would require additional measures. The use of optimal or viable (Mouysset et al. 2014) levels of incentives appear to make it possible to improve this trade-off and more generally the ecological-economic outcomes. In addition to the national incentive-based policy considered here, at least two main alternative policies could be examined. A first option would consist in spatializing the conservation policy by applying payments to landowners based on the location of their parcels or to the density of vulnerable species (current or future). A second option inspired by a the well used command-and-control regulation relies on the use of quota or constraint in terms of land use that implies external, regular controls on LUC at farm scale. Exploring and implementing these options would require more economical and ecological informations than the conservation policy proposed here, reinforcing the interest in further development of prospective tools like the models and scenarios described in this paper.

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