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

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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 that perspective. Here 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. One of the major originalities is to integrate the effect of climate change on the economic drivers of land use using fine-scale data from France. Different economic and conservation scenarios, coupled with a regionalized projection of climate change (IPCC SRES A1B) are compared in terms of impacts on land use and biodiversity over the next four decades. Our analysis indicates that the effect of climate dominates the effects of land use and conservation policy on bird abundances at the national scale. Moreover, global environmental changes turn out to be globally detrimental for biodiversity. Only a moderate number of bird species and locations appear to profit from habitat-based conservation.

Keywords: Climate change ; land use ; conservation policy ; econometrics ; common birds.

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Contents

1 Introduction

Climate and Land Use Changes (LUC) are considered to be two of the main drivers of past and future changes in terrestrial biodiversity (MA 2005, Pereira et al. 2010; Willis and MacDonald 2011). For medium-term prospective analyses (ca. 50 yrs) these two drivers can be treated very differently in terms of scenarios and possibilities for intervention for biological conservation policy. At this temporal horizon, global warming can reasonably be considered as exogenous since climate projections foresee that most of the climate change over this period is already committed (i.e., are relatively independent of greenhouse gas emissions scenarios, IPCC 2007; Rogelj et al. 2012). By contrast, LUC are potentially under much greater control of national and local decision makers and therefore seen as more controllable drivers for conservation policies. However, some of these present and future LUC are likely to be influenced by climate change. It is clear that local opportunities and constraints appear when climate changes and that humans adapt their use of land resources. For example, there are already signs of negative impacts of recent climate warming on corn and wheat yields, and models foresee that future climate change will result in projected northward shifts of maize area in the United States, or rice area in China (Brisson et al., 2010; Lobell et al., 2011; Tubiello et al., 2002; Xiong et al., 2009). Consequently, an efficient conservation policy has to be based both on the direct climate effect on species communities and the indirect effects induced by human adaptations, strategies and public policies (Hannah et al., 2002; Berrang-Ford et al., 2011). It requires the integration of ecological, environmental and anthropogenic dimensions accounting in particular for economic mechanisms. This paper presents an integrated bio-economic model as a way of exploring these interactions. We use a fine-scale analysis of continental France as a case study to demonstrate the insights that can be provided by this type of model.

We use the abundance of common bird species as our biodiversity metric, since birds are often regarded as good general indicators of the state of wildlife and of the countryside, for both scientific and practical reasons (Furness and Greenwood, 1993; Gregory et al., 2005). For our analysis, bird abundance data were extracted from a standardized, volunteer-based monitoring program with a random initial selection of sites that results in habitat-representative sampling efforts. Compared with threat status, population trends are updated more frequently and thus have a higher temporal resolution. Habitat representativity is crucial because it provides coherence with the land use mapping of all cover types in the econometric model about LUC (agricultural areas, semi-natural areas but also urban areas.) A high temporal resolution is necessary for both model calibration and extrapolation to the future. In our analysis, the dynamics of bird species populations are related to climate and habitat changes, based on the principals of Species Distribution Models (SDM). However, we have modeled species population size rather than the probability of presence that is typically predicted by SDM (Araújo et al., 2005; Guisan and Thuiller, 2005; Brotons et al., 2012; Renwick et al., 2012). These models are based on ecological niche theory (Hutchinson, 1978), and assume that habitat and climate requirements can be deduced from current distributions and then distributions and population size can be extrapolated using projections of future climate and habitat changes (Peterson et al., 2011).

To simulate future land use dynamics, an econometric model is used to estimate spatially explicit LUC based on the assumption that land use decisions are functions of economic returns as assessed by private decision makers (Stavins and Jaffe, 1990; Plantinga, 1996; Nelson et al., 2008; Radeloff et al., 2012). Such models have been shown to be consistent with classical economic theory and observations (Lubowski et al., 2008; Lewis et al., 2011). Nevertheless, such models are very demanding in terms of data because knowledge of potential economic return is required for each sampled land plot and each possible land use. We circumvent this constraint by combining aggregated but exhaustive data about land prices and precise data at each sampled land plot about biophysical attributes including topography, land quality and climate. The econometric model is estimated on observed LUC (France, 1993–2003) in order to simulate spatially explicit LUC for different economic scenarios (for a similar exercise in the U.S. but with different data choices, see Radeloff et al. 2012).

The third component of our bio-economic model takes into account the effect of climate change on the economic returns of land within a Ricardian analysis. Based on the seminal work of Mendelsohn et al. (1994) and extended for different regions of the world (see Mendelsohn and Dinar, 2009 for a review), this consists in evaluating the consequences of climate change on land profitability on the basis of the correlations between current land prices and climate variables. Because land price is considered as the net present value of an infinite flow of economic returns, the effect of projected climate on land prices is a proxy for its net effect on the economic returns of land. With this structure in three modelling blocks (SDM, LUC and Ricardian analysis), this integrated bio-economic model is used to simulate future land uses and birds' distributions from the present to 2053 in 10 years time slices.

2 Material and methods

2.1 Data

2.1.1 *Bird abundances*

We used bird 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 in spring (Jiguet et al., 2012). In FBBS, each observer provides the name of her municipality, and a 2×2 km square to be prospected is randomly selected within a 10 km radius from the gravity center of this municipality. In each square, the observer monitors 10 point counts separated by at least 300 m twice per spring (4 to 6 weeks between the sessions, 5 minutes each). Counts were repeated yearly by the same observer at the same points, on about the same date (with a maximum difference of 7 days within April to mid June) and at the same time of day (with a maximum difference of 15 minutes). FBBS data contribute to European official index of biodiversity and have been extensively used to study the effects of climate and LUC on bird populations (Barbet-Massin et al., 2011; Barnagaud et al., 2012), as well as the effects of farmers' preferences (Mouysset et al., in press) and the effects of agro-environmental policies (Mouysset et al., 2011, 2012). To simultaneously smooth annual noise and model the observed dynamics, FBBS data are used at two points of time, 2003 and 2009. For each species and each FBBS square, bird abundances are respectively defined as the maximum number of counts 2002–2004 ($n = 1,031$) and 2008–2010 ($n = 1,380$). FBBS provides also a description of the habitats of the surveyed squares. Even if this information cannot be used to describe the national dynamics of LUC, they appear to be better predictors of the bird population than the aggregation of more exhaustive data at the scale of FBBS squares. So the SDM are estimated with FBBS habitats description and each FBBS observation is weighted in the regressions according to its significance in terms of local land use.

2.1.2 *Land Use Changes*

Data about LUC are extracted from the TERUTI survey which was carried out every year 1992–2003 by the statistical services of the French Ministry of Agriculture. The TERUTI survey counts about 550,000 points for which we know the location in terms of French municipalities: the finest administrative delineation ($n \approx 36\,500$, median area: 10.73 km^2). The TERUTI survey uses a systematic area frame sampling with a two-stage sampling design. In the first stage, the total national area is divided into a 12 × 12 km grid. For each of these 4,700 regular meshes there are 4 aerial photographs which cover 3.5 km^2 each. In the second stage, on each photograph, a 6-by-6 grid determines the 36 points to be surveyed in June by an agent on the ground. Each point corresponds to a homogeneous unit in terms of land use and statistically represents about 100 hectares (ha) at the *département* scale ($n = 95$, median area: 5,880 km^2). On the basis of the detailed classification of land uses (81 items) we attribute to each plot a use among 5 more aggregate items: annual crop, pasture, perennial crop, forest or urban. These data have already be used to estimate econometric LUC models by Chakir and Parent (2009) and Chakir and Le Gallo (2012) but not for the whole of France and at a such disaggregate level. They have been similarly merged with a subset of the avian data that are used here, at the national scale (Devictor et al., 2007, 2008), but not in relation with the economic incentives of landowners' choices.

2.1.3 *Economic returns*

For the estimation of the econometric model of LUC, the price of land is used to compute the expected net returns from different agricultural land uses. Defining land price as the net present value of expected future rents is standard in the economic theory (Ricardo, 1817; Goodwin et al., 2003). This approach, detailed in subsubsection 2.2.3, uses data about land prices that also come from the statistical services of the French Ministry of Agriculture. Yearly prices 1990–2005 are available for three land uses (annual crops, pastures and perennial crops) and for the 713 Small Agricultural Regions (SAR) of France. SAR size ranges from 11 to 4,413 km^2 with an homogeneity in terms of both agro-ecological and economic levels, reducing intra-SAR heterogeneity (Mouysset et al., 2012). For the two others considered land uses – forest and urban – the approximations of economic returns are computed differently and at different geographic scales. For the expected net returns from forest, we use data about wood raw production (in m^3), total forest area (in ha) and wood prices (in current euro per ha), all available annually at the scale of the French *départements*. We compute the expected returns from forest by multiplying the aggregate production by its unitary price and dividing the result by the total forest area of each *département*. Because this calculation provides the net returns per total forested area, it implicitly takes into account that only a part of the forest area is harvested each year (with a harvested share closely related to the length of rotations). It is nevertheless based on the assumption of a myopic agent who makes decisions based on the hypothesis that future returns will be the same as today and neglect production costs. The urban returns are approximated by the population densities at the fine scale of the municipalities on the basis of the national census of French population (source: http://www.insee.fr/en/bases-de-donnees/default.asp?page=recensements.htm, last accessed: February 18, 2013).

2.1.4 *Biophysical attributes*

Biophysical attributes of sampled TERUTI plots include both topographic and climate variables. Topography of each plot was generated by coupling a Digital Elevation Model of France (resolution of 250 meters, see http://professionnels.ign.fr/rgealti, last accessed: February 18, 2013) with the spatial geo-referencement of plots. Within a Geographical Information System (GIS), we calculated the elevation, the slope, the roughness and the exposition of each TERUTI sampled plot. Soil quality variables were extracted from the French soil database developed by the National Institute for Agricultural Research and matched by GIS. The initial data are available at the 1:1,000,000-scale (Jamagne et al. 1995, http://www.gissol.fr/programme/bdgsf/bdgsf.php, last accessed: February 18, 2013) and they were downscaled to a 1-km grid with pedotransfert rules (Cheaib et al., 2012). They provide measures of the agricultural fertility of plots: plant available water capacity and soil depth.

We use historical (1990–2010) and projected (2010–2053) climate data, both available at the same spatial resolution (8 × 8 km rasters) with a smooth transition between historical and future climate. Climate data include 13 variables about temperatures (annual means, maximum and minimum, bird breeding period means April–August and seasonality approximated by standard deviation), precipitations (annual means, maximum and minimum, breeding period means and seasonality), solar radiation (breeding period means), relative humidity (breeding period means) and wind (breeding period means). Regionalized climate scenarios are based on the Intergovernmental Panel of Climate Change's SRES A1B greenhouse gas emissions scenario A1B coupled with the *Météo-France Arpège* climate model (Déqué, 2007). Regionalized climate projections were produced with a multivariate statistical downscaling methodology, which is able to generate local time series of temperature and precipitation, and other climatic variables at different sites (Boé et al., 2009). The model is based on large-scale circulation predictors, here the mean sea-level pressure field, as well as the 2-meter temperature averaged over France. It starts from regional climate properties to establish discriminating weather types for the chosen local variable. Intra-type variations of the relevant forcing parameters are then taken into account by multivariate regression using the distances of a given day to the different weather types as predictors. The final step consists of conditional re-sampling (for further details in climate downscaling see Boé et al., 2009 and Cheaib et al., 2012).

2.2 Models

2.2.1 *Species Distribution Models*

Bird populations are modeled with Species Distribution Models (SDM) that are viewed as providing a first approximation of the potential impact of climate and habitat changes on biodiversity (Pearson and Dawson, 2003). For a general description of the method, we note μ_{tqs} the abundance of species s in the FBBS 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 $\lambda_s(\cdot)$ are spline-based smoothing functions with an endogenous structure as it is common for Generalized Additive Models (Hastie and Tibshirani, 1990). They have to be estimated, as the scalars δ_s that capture the linear growth 2003–2009 for each species s, all other things equal. $\mathbf{c}_{qt}$ stands for the values at location q and time t of the two first axes of a principal component analysis on the matrix of climatic variables. The Figure SM1 of Supplementary Material (SM) shows the locations of the initial variables in terms of their principal axes that account for 87% of variance. $\mathbf{h}_{qt}$ is the vector of habitat variables including a fragmentation index, $\mathbf{x}_q$ represents a vector of topographic variables while $\mathbf{z}_q$ is the spatial coordinates of the gravity center of each FBBS square. Including the spatial coordinates inside the smoothed function 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 birds' 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).

2.2.2 *Econometric model of Land Use Changes*

We have reduced land use types to five ($L = 5$) exhaustive and mutually exclusive categories. In our case study, land uses refer to annual crop, perennial crop, pasture, forest and urban. Landowners are assumed to choose LUC in order to maximize their utility and these choices are assumed to be independent for each parcel. With this latter assumption, we can associate each plot of land with a distinct decision maker. In particular, a stylized landowner i chooses the use ℓ^*_{it} on a plot if this provides the highest utility from all uses that are possible. The following formula:

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

is connected to the behavioral assumption of rationality. But rationality is not a necessary condition, as Train (2009) explains: "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." Utility $u_{i\ell t}$ is net of conversion costs from the previous land use (in period $t-1$), we comment this point later. This formulation for utility is forward-looking and allows the possibility of multi-year LUC as perennial crop, forest or urban. In the literature (Plantinga, 1996; Lubowski et al., 2008), utility is assumed to be the expected one-period net returns that come from a dynamic optimization problem. 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 ($\forall \ell = 1,\dots,L$) and for each sampled plot ($\forall i = 1,\dots,I$), we assume:

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

Where $\widehat{\mathbf{r}}_{it}$ is the computed vector of net returns in t for each possible land uses on plot i. Because these variables are only available at the scale of the SAR, they are crossed with climate $\mathbf{c}_{it}$ and biophysical variables $\mathbf{x}_i$ to allow plot-level deviations from the aggregate returns. These two latter vectors come from a dimension reduction of initial variables by principal component analysis (see Figure SM1 of SM). Conversion costs between uses are taken into account (and proved to be strong determinants) by including $L-1$ dummy variables representing the previous land use of plot i: $\mathbf{h}_{it-1}$. So, the vector $\boldsymbol{\eta}_\ell$ provides estimates of the costs to change to land use ℓ. Each vector of coefficients to estimate $[\alpha_\ell;\boldsymbol{\beta}_{\cdot\ell};\boldsymbol{\eta}_\ell]$ is proper to a 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 considered land use.

Because all the sources of landowner's utility cannot be observed, an error term $\epsilon_{i\ell t}$ is included in eq.(3). The stochasticity of the model is only related to these unobserved components of utilities and their associated densities. McFadden (1974) identifies three standard hypothesis about errors that allow to obtain a multinomial logit model: independence, homoscedasticity and extreme value distribution (i.e., Gumbel). With these hypothesis, one can show that the probabilities have simple closed forms, which correspond to the logit transformation of the deterministic part of the utility ($\bar{u}_{i\ell t} \equiv u_{i\ell t} - \epsilon_{i\ell t}$). The probability that the land plot i is in use ℓ at the period t is:

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

The estimation was performed using `nnet 7.3` and `mlogit 0.2` on `R`. Another critical part of the model is that the unobserved factors have to be uncorrelated over alternatives and periods, as well as having the same variance for all alternatives and periods. These assumptions, used to provide a convenient form for the choice probability, are found to be not restrictive (homoscedasticity cannot be rejected by a score test, p-value= 0.283). Moreover, these hypothesis are associated with the classical restriction of Independence of Irrelevant Alternatives 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%. This means that the 3 formers choices can be dropped from the choice set without modifying significantly the parameters of the model (i.e., they are robust to the IIA restriction) a property which is not true for the 2 latter.

2.2.3 *Models of economic returns*

As noted above, the price of land is used to compute the expected net return from land use. To understand this, land is considered as a classical fixed asset. This implies 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 that keeping it in its current use allows to earn. Assuming flat interest rates $\tau_t = \tau$ and flat rates of capital gains $g_t = g$, this reads as follows:

$$v_{\ell t} = \sum_{s=1}^{\infty} \frac{\mathbb{E}_t(r_{\ell t+s})}{\Pi_{j=1}^{s}(1+\tau_{t+j})} = \sum_{s=1}^{\infty} \frac{\mathbb{E}_t(r_{\ell t+s})}{(1+\tau)^s} = \sum_{s=1}^{\infty} \frac{\mathbb{E}_t(r_{\ell t+1})(1+g)^s}{(1+\tau)^s} = \frac{\mathbb{E}_t(r_{\ell t+1})}{(\tau-g)}, \quad (5)$$

The expectation operator at t is noted $\mathbb{E}_t$, and previous equalities use the well-known property of the sum of infinite geometric series. Thus, knowing or making an assumption about the difference between the interest rate and the rate of capital gains $(\tau - g)$ is sufficient to compute the expected return of a land plot on the basis of its observed price: $\widehat{r}_{\ell t} = (\tau - g) \cdot v_{\ell t}$. This result depends strongly on well-functioning (i.e., competitive and balanced) markets and so has to be considered as a theoretically-consistent first approximation.

To model the effect of climate change on land prices $v_{\ell t}$ or, equivalently, on the expected net returns $\widehat{r}_{\ell t}$ of annual crop, pasture, perennial crop and forest, we use a Ricardian analysis (Mendelsohn et al., 1994). The Ricardian equations relate the economic returns of land to climate, other biophysical variables and geographical coordinates. The relation is specified as follows:

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

with $y_\ell(\cdot)$ is a spline-based smooth function with endogenous structure which depends of the considered land use. Thus, these GAM functions and the γ_ℓ are estimated on the cross-sectional variations between SAR and the time series 1993–2003, accounting for the capitalized value of climate and time in land returns. The models are estimated separately for annual crop, pasture, perennial crop and forest using GAM with a distribution from the Gaussian family with natural logarithm link (Wood, 2006). For the dynamics of the urban returns, we use the spatialized previsions of population growth by INSEE. Because demographic data are available at the *département* scale, they are downscaled by assuming that each municipality keep a constant proportion of the aggregate values.

2.2.4 *Simulation of scenarios*

Our scenarios differentiate themselves by the dynamics of the deterministic part of utilities of eq.(4). The estimated logit regression function $\widehat{f}_\ell(\cdot)$ and the biophysical variables $\mathbf{x}_i$ stay constant between scenarios. But, depending on the considered scenario, the economic returns $\widehat{\mathbf{r}}_{it}$ and/or the climate variables $\mathbf{c}_{it}$ are allowed to change. We consider 5 scenarios that are presented in Table 1. They vary according to three dimensions: the extrapolation of current trend, the inclusion of climate change and the presence of a conservation policy.

Table 1: The differences between scenarios in terms of factors from species distribution and land use change models

Scenario	Factors accounted for in models	
	Bird abundances	Land Use Changes (LUC)
S0	Trend + Climate Change	Constant
S1	Climate + Trend + LUC	Continued trend only
S2	Climate + Trend + LUC	Trend + Climate Change
S3	Climate + Trend + LUC	Trend + Payments for pasture
S4	Climate + Trend + LUC	Trend + Climate Change + Payments

Notes: Simulations of bird population 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 focusing on permanent pastures. See in the text for the details of the conservation policy.

Once the LUC econometric model is estimated, the direct predictions (without changing exogenous variables) consist, for each plot i, in a fitted probability vector $\widehat{\mathbf{p}}_{it}$ of being in each 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. Remembering that each TERUTI observation counts for 100 ha, the predicted probabilities can be easily converted into predicted LUC. As an example, consider a plot 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 (probabilities $\widehat{\mathbf{p}}_{i1}$ are in the order annual crop, pasture, perennial crop, forest, urban). Land use at $t = 1$ 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).

For the others 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 plugged into the logistic equations (4). For S2, climate variables $\mathbf{c}_{it}$ are implemented in the Ricardian equations

(6) as in the logistic equations (4). For both scenarios, we predict a probability matrix of land use in $t = 2$ conditionally on previous land use: $\widehat{\mathbf{h}}_{i2} = \widehat{\mathbf{p}}_{i2}(\mathbf{h}_{i1})$. One has nevertheless to note that this step in the simulation is facilitated by the knowledge of the previous use for each surveyed plots by the 2003 wave of the TERUTI survey: $\mathbf{h}_{i1}$. Things are different to simulate LUC after the period $t = 2$ for which we do not have a single previous use for each plot: we only know a vector of probabilities: $\widehat{\mathbf{h}}_{i2}$. So the next LUC, for $t = 3$ but equally for $t = 4$, $t = 5$ and $t = 6$, are computed differently. 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 $\mathbf{1}_k$ is a $1 \times L$ vector with the k-component equals to 1 and the others to zero. In other words, variables describing land use are still 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 conservation policy (for S3 and S4) is straightforward. Here, to keep the paper short, we describe only the results to a permanent payment of 200 euros/ha for the pasture. Different taxes and/or subsidies on other land uses can also be implemented with our model, we let it for future researches. This conservation policy consists, for $t > 1$, in increasing the rents for pastures ($\ell = 3$) used to fit transition probabilities:

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

For the others uses, the respective economic returns of S3 and S4 are the same as S1 and S2. For all scenarios, LUC are used in the SDM of eq.(1) to predict bird abundances at the sames spatial and temporal scales. At this final stage, these LUC effects are coupled with the direct effect of climate change on bird distribution. To evaluate the effects on birds we use an abundance-based index: the geometric mean of current 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, principally the France to obtain national dynamics or the 12 × 12 km TERUTI mesh to optain maps. Applied to farmland specialists species, this index is the well-used European Farmland Bird Index but we use it equally on birds species as a whole and for different habitat specializations: generalist, forest and urban. Because this index aggregates potentially heterogeneous species' trends, we use the formula from Gregory et al. (2005) to compute the associated standard errors.

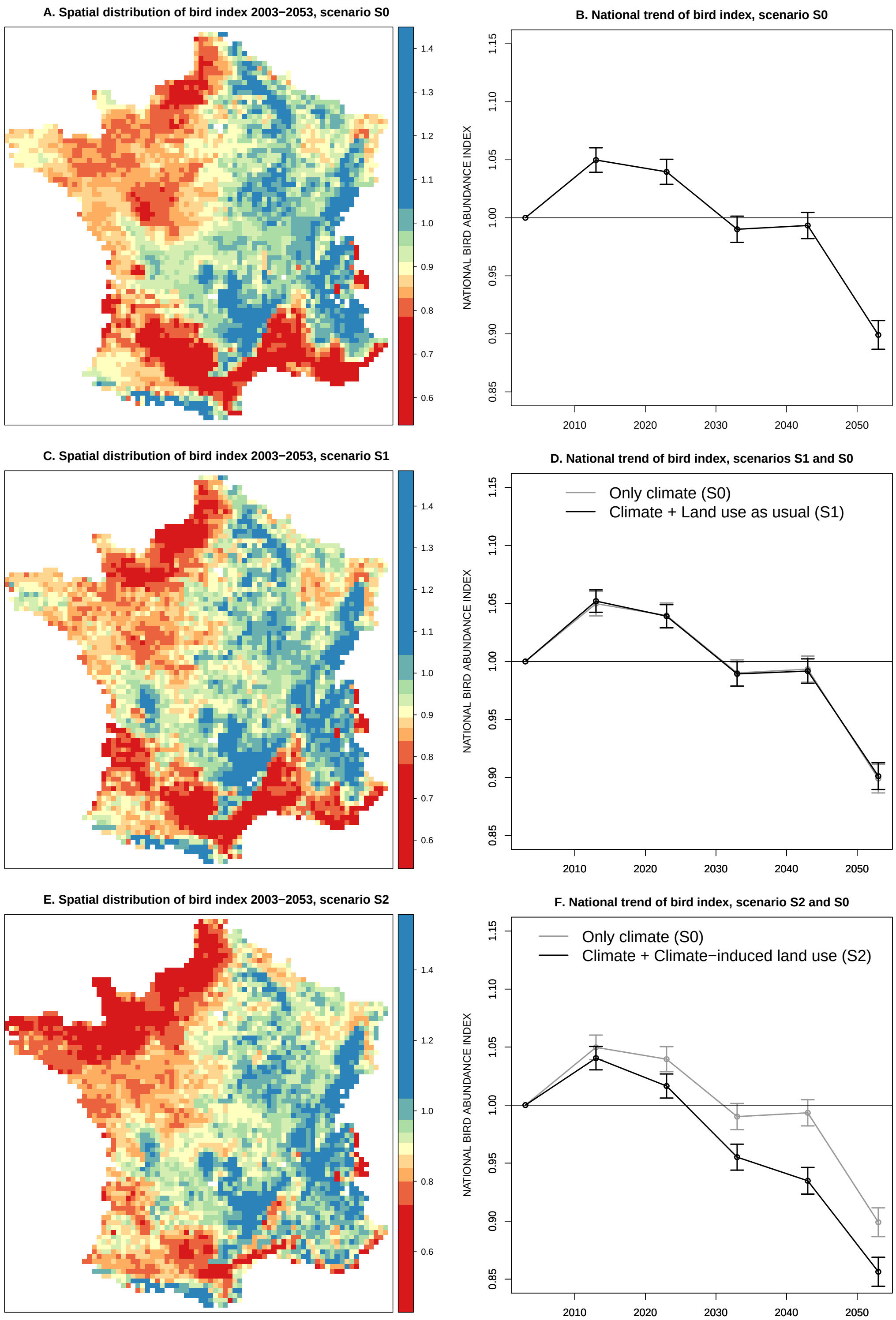
3 Results

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

The first scenario consists in predicting the effect of climate change on bird populations, modifying only climate in the SDM. This means that land use is considered as constant. Under the IPCC SRES A1B regionalized climate projection used here (Cheaib et al., 2012), the annual temperature of France is projected to increase by + 2.02°C ± 0.23 s.d. up to 2053. The annual cumulative precipitation is projected to decrease by − 13.40 mm ± 6.3 s.d., the relative humidity to decrease by − 1.69 % ± 1.2 s.d. and the solar radiation to increase by + 17.10 J ± 14.4 s.d. As displayed in the Panel B of Figure 1 from a national viewpoint, the effect of climate change on the aggregate bird index is first positive (+ 5% up to 2020), not significant for 2030–2040 and strongly negative from 2040 onward (− 10% at 2053).

The spatial precision of the projected climate (8 × 8 km) allows us to model more precisely

Figure 1: The effects of climate and land use changes on the index of bird abundances for the scenarios without conservation: S0, S1 and S2.



than usual the geographical shifts in bird distributions. As the panel A of Figure 1 shows, the Mediterranean coast at the southeast and the center of the southwest are two regions of important decline in bird populations. Some important (even if less strong) detrimental effects appear as well in the northwest of France. In contrast, bird populations in the continental part of the country – the east and the center – have high 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 bird population dynamics. The Figure SM2 of SM differentiates the direct effect of climate according to species' preference in terms of habitats. It shows that climate change up to 2053 is significantly detrimental for generalist species (about − 10%), forest specialists (about − 30%) and urban specialists (about − 2.5%). In contrast, the model predicts that the abundances of farmland specialists increase by about + 10% over this period, even if the confidence interval is larger than the others. 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. The Figure SM3 provides the individual rates of variation for each bird species abundances 2003–2053. Climate change significantly impacts the large majority of species: the variations of only 2 species are not significant, 21 species increase and 39 decrease.

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

This first scenario of LUC was simulated by extrapolating the 1993–2003 trends of economic returns (see subsubsection 2.2.4). It is coupled with the previous S0 effect of climate change on birds. Panel (a) of Table 2 presents the national land allocation 2003–2053 with decennial steps. The main insights are, as for the previous decade, the increase of annual crop, forest and urban area (respectively + 3.17%, + 9.11% and + 33.4%) and the decrease of pasture and perennial crop area (both of − 17.7%). In relative terms, the urbanization of land is the most notable trend, as in Haim et al. (2011). The dynamic of annual crops is the more subtle with a small loss 2003–2013, an increase 2013–2033 and a stagnation 2033–2053.

Table 2: National acreages of land uses (in thousand hectares) and the associated growth rates for scenarios S1, S2, S3 and S4

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
Δ(%)	− 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
Δ(%)	+ 177	+ 27.15	− 55.5	+ 1.71	+ 60.1	+ 83.7	+ 16.15	− 19.36	− 9.43	+ 23.5

Notes: In columns: ANCR for Annual Crops, FORES for Forests, PECR for Perennial Crops, PAST for pastures and URBA for urban. The two last rows, named Δ(%), present the growth rates 2003–2053.

The effect of LUC in the scenario S1 is globally neutral concerning the dynamics of the national bird index: the differences with S0 are small and not significant (see Panel D of Figure 1). In S1, the aggregate bird index is shaped exclusively by climate change. Spatially, the general structure is maintained but there is some mitigation at certain parts of the south of France and an amplification at the northwest (see Panel C of Figure 1). To disentangle the effects of S1 LUC from the climate effects, the Figures SM4 and SM5 present the net effects of S1 LUC with constant climate. It appears that S1 LUC effects are much more smooth and homogeneous between species with the same habitat preferences (relatively to the effects plotted in Figure SM2). 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 grow significantly for 15 species as a result of S1 LUC, 10 decrease significantly and 37 do not exhibit any significantly evolution.

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

The endogenisation of the effects of climate on the economic returns of land by the Ricardian models is presented in Table 3. Up to 2053, the returns are predicted to increase for annual crop (md= + 116.8%), for pastures (md= + 73.81%) and perennial crop (md= + 13.35). The median increase of the density of population is + 28.31% but the median rate of variation for returns from forest is negative: − 13.18%. Climate change is also found to increase the heterogeneity (measured by Standard Errors) in terms of economic returns for annual crops, pastures and urban.

Table 3: The Ricardian effects of climate change on the economic returns from land: amounts in money and in variations

	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

Notes: 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 and variations are expressed in %. In row: ANCR for Annual Crops, FORES for Forests, PECR for Perennial Crops, PAST for Pastures and URBA for Urban.

The Panel (c) of Table 2 presents the consequences of such variations of economic returns in terms of LUC. Except for perennial crops, climate-induced LUC are in the same directions as in 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 concerns few locations already specialized in perennial crops (southeast in particular). The important decrease of pastures (– 55.5%) is mainly explained by the substitution for annual crops and urban. The growth rate of urbanization in S2 is twice the rate of S1 even if the same scenario in terms of population growth is used. This can be explained by the fact that higher temperatures are in general associated with bigger houses and bigger gardens in France (to enjoy warmer temperatures), so global warming is projected to increase urbanization (Haim et al., 2011).

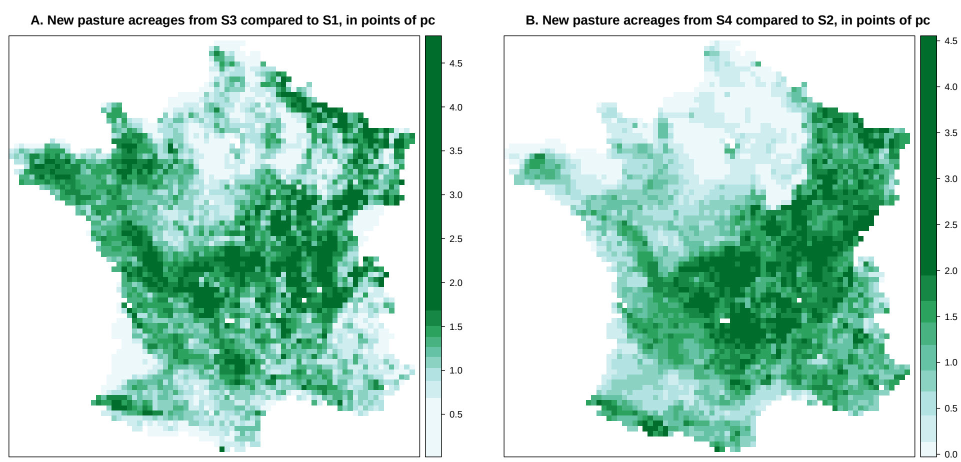
The Panel F of Figure 1 shows that climate-induced LUC amplifies the negative effect of climate change on the aggregate bird index. With climate-induced LUC, the national bird index shows a decrease of 14% of abundances in 2053, relatively to 10% in the case of constant land use S0. Panel E of Figure 1 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 implies a northern shift of annual crops and an increase of urban and perennial crops in the south that explain these results.

The isolated effects of S2 LUC on birds are shown in Figures SM6 and SM7, according to habitat preferences of bird species and for each species separately. It appears that only urban specialists benefit from climate-induced LUC: + 10.5%. The others present a significant decrease in abundance for 2053: respectively – 5%, – 7.5% and – 8.5% for generalist, farmland and forest specialists. The raw effects of S2 LUC are negative and significant for 41 species and positive for only 12 species. The latters are all urban specialists except the Eurasian skylark (*Alauda arvensis*) that is a farmland specialist.

3.4 Climate change with conservation policy (scenarios S3 and S4)

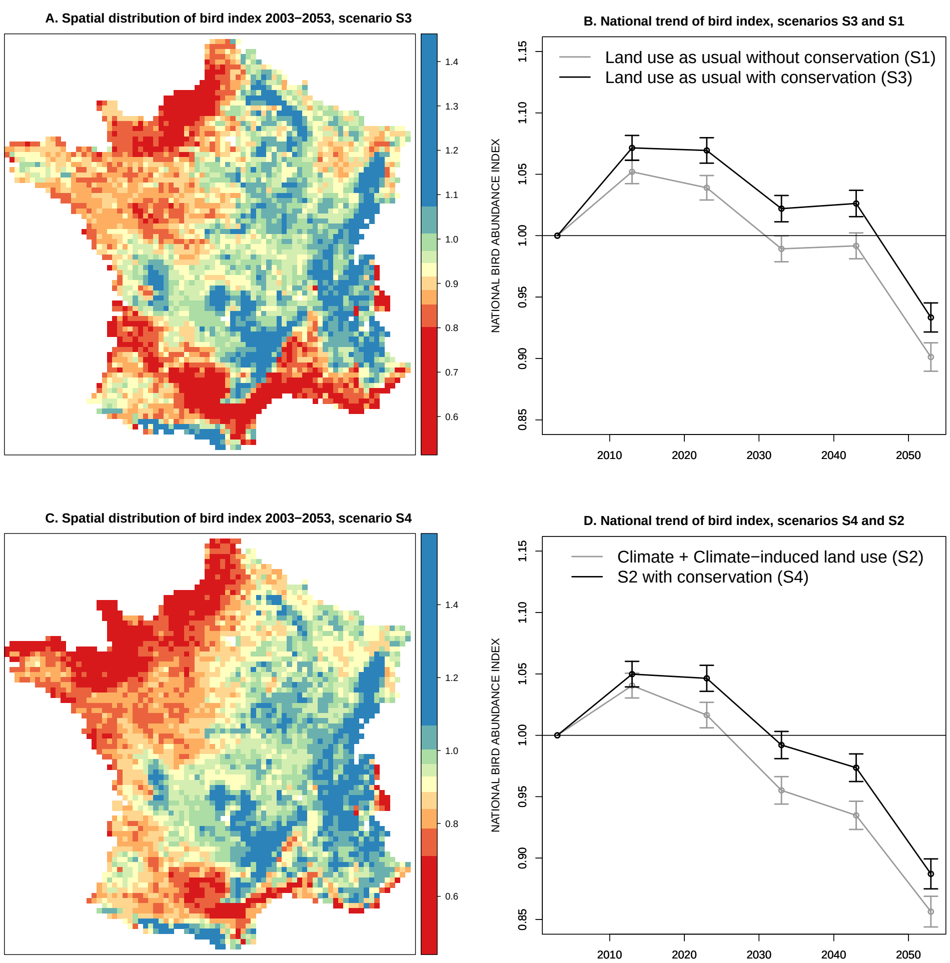
Coupled with S1 to produce S3, the annual payment of 200 euro/ha for pasture is sufficient to reverse the predicted decline of pasture in the next decades, see the Panel (b) of Table 2. This payment involves a net increase of + 22.6% of pastures in the period 2003–2053. In S3, the urbanization is still positive but moderate (+ 17.5%) relative to S1. Pastures induced by such a conservation strategy (new pastures but also pastures that are not converted) replace principally annual and perennial crops in the scenario S1. Even if the conservation scenario negatively affects forest acreages, the loss is small: − 2.15%. The spatial distribution of these conservation-induced pastures are presented in the Panel A of Figure 2. Areas of annual crop specialization (around *Paris* at the northern center) and of forest specialization (extremes southwest and southeast) are not heavily impacted by the conservation which are well spread over locations.

Figure 2: The net effects of the conservation payments of 200 euro/ha on pastures in scenarios S3 and S4, relative to S1 and S2 respectively



However, coupled with S2 to obtain S4 (i.e., taking into account climate change impacts on LUC), the same payments for conservation are not able to reverse the loss of pastures, see the Panel (d) of Table 2. Nevertheless, the predicted loss is highly mitigated relatively to S2, and the 2053 acreages of pasture with conservation policy (S4) are near than twice the acreages without conservation (S2). The payments for pasture coexist with an increase of annual crops because, as we have already seen, crops returns increase both by the extrapolation of trends and the benefit from climate change by the Ricardian effect. Conservation payments decrease urbanization even though this land conversion remains high (+ 23.5%). This scenario S4 presents the highest loss of forest acreages (− 9.4%) both because of the decrease of the returns of forests from climate change and the competition with pastures that come from conservation. In this scenario, conservation-induced pastures are clearly spatially segregated (see the Panel B of Figure 2). The east and the center of France concentrate the principal part of these pastures, leaving the northwest weakly impacted by the conservation.

Figure 3: The effects of climate, land use changes and conservation policy on the index of birds abundances for scenarios S3 and S4.



For both conservation scenarios S3 and S4, the payments for pasture allow to significantly increase the national bird index but not sufficiently to counteract the negative effects of climate change (Panels B and D of Figure 3). The national trend stays shaped by climate change (i.e., first a small increase then a bigger decrease) even if the differences that come from conservation are statistically significants. For S3, the negative effects of climate are delayed to 2045 instead of 2030 for S1. For S4, the conservation implies 2053 birds' abundances close to S0 (about − 10%), indicating that conservation allows to counteract globally the negative effects of climate-induced LUC. It is also interesting to show that the effects of the 200 euros/ha conservation 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 SM8 and SM9 present the net effects of both scenarios with conservation on bird species individually. For S3, the effects of conservation are generally positive. They involve detrimental effects only for 10 species of all habitat preferences, and species with negative effects from S1 are not particularly targeted. The biggest improvements due to conservation concern 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 of the bottom of the Figure SM9 that are declining strongly in S2. This is a kind of mitigation effect from habitat-based conservation, but clearly insufficient to counteract the patterns implied by climate change.

4 Discussion

4.1 Ecological models

We show that the dynamics of bird populations facing climate change vary according to both their location within their current climatic niches and the land use corresponding to their future climatic niches. Our results clearly show that the former source of variation is stronger than the latter. A first explanation for this result is simply that climatic variables have stronger effects in SDM that habitat and topographic variables. So, the climate side of our scenarios is the most important driver of the spatial dynamics of common birds. The second explanation is that LUC of our scenarios are not directly operated in relation to birds dynamics. LUC and conservation policy could potentially have stronger effects if they were deliberately shaped for bird conservation and if the climate-induced shifts in bird distributions were taken into account in land use decisions. But, even if conservation policy could be better designed, the observed magnitude of differences between scenarios suggests that it would be very difficult for land use allocation schemes to overcome the large climate signal. This result is in contrast to the commonly held belief that land use change will remain the dominate driver of bird diversity dynamics (Jetz et al. 2007) or biodiversity dynamics in general (Periera et al. 2010) over the coming century. While this land use may remain the dominant driver at global scales, our work suggests that this may not be the case in many areas where land use and biodiversity dynamics are not mediated by large scale deforestation and conversion of natural systems to production systems.

Omitting large parts of a species range when modeling its distribution can overestimate the risk of local decline or extinction, as it does not consider all possible environmental conditions where a species can survive. Current developments of SDM for animals try to disentangle the effects of various environmental variables on population dynamic parameters, e.g., climatic impacts on survival, reproductive success and dispersal. Developing such models will provide more efficient inferences for policy decision, by better targeting potential expected improvements. A few studies already tried to consider realistic dispersal scenarios for birds predicted to shift their range polewards, but accounting for dispersal did not change the estimates of impact predictions at a national scale (Jiguet et al., 2013). As regards biodiversity metrics, the use of geometric mean of current abundances (e.g., taxonomic diversity) is not totally satisfying. The current biodiversity crisis could impact the future potential of evolutionary processes, so that the impacts of global change on phylogenetic diversity should be estimated. Similarly, as long as ecosystem processes are those important for the resilience of the global biological diversity, future investigations should concern the potential impacts of global change on functional diversity. Species interactions are shaping community dynamics and functions, and integrating the architecture of mutualistic or trophic networks will necessarily improve predictions (Thébault and Fontaine, 2010).

4.2 Econometric models

Our empirical model of LUC provides a means to examine the effects of returns from land and economic-based policies (i.e., acreage payments) on land use decisions. We show that changing the returns from land is sufficient to induce significant variations in terms of LUC, relative to the scenario with extrapolated trends. Through their influence on capitalized values into land returns, climate variables are also proved to be strong determinants of LUC. With our regionalized projections, the net effect of climate change is to increase urban, annual and perennial crop acreages, at the expense of pastures and forests. These results are shared by many projections about LUC but the fine resolution of the initial data and the extrapolation by the modelisation of landowners' choices allow us to obtain a particularly high spatial resolution.

Although our LUC model provided promising results, it could be enhanced in several ways. An area for future research is the development of data and methods that could help to estimate more precise econometric models of LUC. One possible improvement of our model is to take explicitly into account spatial autocorrelation of the outcome variables, the residuals or both. The challenge, then, is for land use modeling to take into account time and space within a unified framework. In this perspective, the methods developed by Sidharthan and Bhat (2012) seem to be promising and are a good alternative to a Bayesian framework or an estimation by simulation methods which are quite intensive in terms of computation.

Concerning the Ricardian models, there is legitimate concern that extrapolation too far into the future may exceed the valid range of use of econometrics. It is especially striking when applied to novel climates that do not occur in the data used to estimate the model. However, alternatives such as process-based modeling approaches often suffer from a lack of data to properly constrain parameterization and may suffer from overtuning, so choosing between modeling approaches is not clear-cut. These issues are very similar to those that arise when comparing empirical and process-based SDM, for which model selection is difficult to make based on objective criteria (Cheaib et al., 2012). A recent multi-study analysis of climate change impacts on African agriculture indicates econometric approaches give results that are coherent with statistical and processes-based approaches over the time frame examined in our analysis (Müller et al., 2011).

4.3 Climate scenario

For this analysis, we have used a single climate projection and, therefore, there is a substantially broader range of projected climate changes than we have explored. This means that there is also substantially higher uncertainty in projections of bird population change and LUC than presented here. As noted in the introduction, climate projections from the present to mid-century differ more between climate models than between emissions scenarios, especially in the IPCC AR4 SRES-based climate model ensemble (Knutti and Sedláček, 2012). The most recent IPCC AR5 RCP-based climate model ensemble projections give even broader ranges of warming and precipitation than the AR4 projections, but the multi-model ensemble averages are very similar to AR4 projections at both global and French scales (Knutti and Sedláček, 2012; Diffenbaugh and Giorgi, 2012). Large uncertainty, especially concerning future precipitation regimes must be kept in mind, since modeled populations and distributions of birds and LUC appear to depend on temperature and precipitation (see Table SM1 and SM2 of SM). The climate projections that we have used are, however, close to the mean of the AR4 and AR5 multi-model climate projection ensembles over the period that we have studied.

It has been shown that climate impacts are highly dependant on the spatial scale of climate projections, especially in mountainous areas (Franklin et al., 2013). Thus, given the importance of altitudinal related climate variation in determining both bird and LUC responses to climate change, regionalized climate is an essential component of analyses of interactions between climate, LUC and policy in this type of study. The statistical climate downscaling method used in this study provides a much finer spatial scale for time series climate data (ca. 8 km) than global scale (0.5° = ca. 110 km latitude for high resolution data sets) or many regional scale projections (ca. 20 km, Mitchell and Jones, 2005). The downscaled climate is also much better tested against French climate data (Boé et al., 2009) than frequently used downscaling methods based on the WorldClim dataset (e.g., Franklin et al., 2013).

4.4 Conservation policy

Our results suggest that projections of future species distributions, and also management options and conservation assessments, cannot be based on the assumption of a uniform response to climate change across a species range or at range edges only. This illustrates a challenge for the conservation policy that has to reflect this heterogeneity of bird and LUC responses. Incorporating the uncertainty that comes from the data and the models is another policy challenge that will complicate conservation schemes and highlights the need for conservation schemes that leave substantial flexibility for corrections over time. However, the conservation policy has to be simple in order to be understandable for landowners and to avoid prohibitive implementation and monitoring costs. The economic incentives proposed in this paper are in line with these objectives. Here, we limit the conservation policy of a fixed-amount payment for pasture at the national scale. We have also tested another amounts of payments for pasture (100 euro/ha and 300 euro/ha) without observing any change in the relative spatial distribution of effects. The national acreages of pasture are growing with the amounts of payment but the relative shares at different scales stay constants. Determining the optimal level of payments for pasture is outside the scope of this paper.

In contrast to the incentive-based, national policy studied here, at least two main alternative conservation policies could be implemented at low cost. The first possibility is to keep the economic logic of conservation payments but apply varying payments to landowners based on the location of their parcels or the presence of vulnerable species (current or future). The second possibility is the well-used command-and-control approach that implies external, regularly and not generally compensated constrains on LUC. Both would require more economics and ecological information than the conservation policy implemented here, reinforcing the interest of prospective tools like the models that we develop here. In particular because climate-induced LUC could have positive effects on biodiversity locally, they have to be anticipated by conservation policies so that they do not target areas that are not vulnerable. In the same vein, spatially targeted conservation policies need to take into account the shift in species distributions as a result of climate change, to not target areas that would not be viable.

4.5 Conclusion

We have compared 5 different integrated scenarios from now to the next 4 decades, using IPCC climate, economic and conservation projections. The explicit structure of our bio-economic model allows to study the climate-induced LUC resulting from the economic returns of land and a conservation policy consisting of annual payments to promote permanent pastures. Three main questions have been addressed:

(i) What are the probable effects of climate on common bird abundances?

(ii) Does climate-induced LUC mitigate or amplify the effects of climate?

(iii) What are the effects of payments in order to have more eco-friendly LUC?

For (i), we found a negative national effect of climate change on bird abundances at 2053. This effect is strong relative to the effect of projected LUC. Locally, it causes a greater elevation shift than northern shift in the distribution of birds. For (ii), we found that climate-induced LUC amplify the negative direct effect of climate on birds. This is not the case everywhere, with some, particularly southern, locations that could benefit from such LUC. The answer to question (iii) is more complex, because we found that a conservation policy based on relatively high payments to promote pastures can not counteract the globally negative effect of climate on certain locations and certain species. We do not find any significant correlation between the growth of bird abundances with and without conservation, both at the spatial and the species scales. We interpret that as the positive effects of incentive-based conservation do not match particularly the vulnerable locations and species.

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List of Tables

List of Figures