Ecological Applications, 23(1), 2013, pp. 96–109

How does economic risk aversion affect biodiversity?

L. Mouysset,[1,2,3] L. Doyen,[1] and F. Jiguet[1]

[1]*CNRS, CERSP, UMR 7204 CNRS-MNHN-UPMC, 55 rue Buffon, 75005 Paris Cedex, France*
[2]*INRA, SADAPT, UMR 1048 INRA-AgroParisTech, 16 rue Claude Bernard, 75005 Paris Cedex, France*

Abstract. Significant decline of biodiversity in farmlands has been reported for several decades. To limit the negative impact of agriculture, many agro-environmental schemes have been implemented, but their effectiveness remains controversial. In this context, the study of economic drivers is helpful to understand the role played by farming on biodiversity. The present paper analyzes the impact of risk aversion on farmland biodiversity. Here "risk aversion" means a cautious behavior of farmers facing uncertainty. We develop a bio-economic model that articulates bird community dynamics and representative farmers selecting land uses within an uncertain macro-economic context. It is specialized and calibrated at a regional scale for France through national databases. The influence of risk aversion is assessed on ecological, agricultural, and economic outputs through projections at the 2050 horizon. A high enough risk aversion appears sufficient to both manage economic risk and promote ecological performance. This occurs through a diversification mechanism on regional land uses. However, economic calibration leads to a weak risk-aversion parameter, which is consistent with the current decline of farmland birds. Spatial disparities however suggest that public incentives could be necessary to reinforce the diversification and bio-economic effectiveness.

Key words: agriculture; biodiversity; bio-economic modeling; diversification; economic drivers; farmland birds; France; risk aversion; sustainability.

Introduction

Significant decline of biodiversity in European farmlands has been reported for several decades. Numerous studies point out spatial and temporal correlations between farmland biodiversity and agricultural changes (Chamberlain et al. 2000, Donald et al. 2001, Wretenberg et al. 2007). Modern agriculture and associated intensification of practices have been identified as major drivers of this erosion in farmland biodiversity. The breeding bird populations are particularly vulnerable to global agricultural change (Krebs et al. 1999, Chamberlain et al. 2000). Such a negative effect is due mainly to a degradation in habitat quality altering nesting success and survival (Benton et al. 2003). In this context, the European Union has formally adopted the Farmland Bird Index (FBI) as an indicator of structural changes in biodiversity (Balmford et al. 2003).

A challenge to reach sustainability for agricultural land use is therefore to reconcile farming production and farmland biodiversity. Usual approaches to achieve such multifunctional goals for farming rely on public policies (Pacini et al. 2004) or economic incentives (Drechsler et al. 2007*b*, Mouysset et al. 2011). For Alavalapati et al. (2002) and Shi and Gill (2005), financial incentives are essential to convincing farmers to adopt eco-friendly activities. These policies modify the farmer's choices and thus impact both the habitat and the dynamics of biodiversity (Doherty et al. 1999, Holzkamper and Seppelt 2007, Rashford et al. 2008). In this perspective, many public policies including agro-environmental schemes have been developed by decision makers. However, fifteen years after the initial implementation of such instruments at a large scale, their ability to enhance biodiversity remains controversial (Vickery et al. 2004, Kleijn et al. 2006, Butler et al. 2009).

In this context, exploring some microeconomic characteristics could be helpful to understand the impact of farmer behavior on biodiversity and to eventually improve the effectiveness of public policies. In particular, some studies focus on the farmer's microeconomic features, treating them as forms of risk aversion (Hardaker 2000, Lien 2002). *Risk aversion* is a concept used in psychology, economics, or finance to describe cautious behavior when facing uncertainties. It is related to the preference of a person for a certain, but possibly low, payoff as compared to an uncertain, but potentially higher, payoff. This concept is broadly applied in finance and portfolio theory. Typically a risk-averse investor will put his money into a bank account with a low but guaranteed interest rate, rather than into a stock that may have high expected returns, but also involves a chance of losing value. In line with this, it turns out that *diversification*—namely, the allocation among different financial assets—is a relevant strategy for mitigating risks. In the case of agriculture, theoretical models

Manuscript received 10 October 2011; revised 21 May 2012; accepted 22 May 2012; final version received 14 June 2012. Corresponding Editor (ad hoc): A. J. Hansen.

[3] E-mail: mouysset@mnhn.fr

(Quaas et al. 2007) suggest that in the case of rangelands an adequate risk aversion may bring farmers to adopt sustainable choices. The underlying mechanism is that risk-averse farmers maintain important agrobiodiversity (i.e., a genetic diversity) in their farming system as a way of managing increasing economic risk. In other words, risk-averse farmers will plant a variety of crop types to reduce risk of failure of a unique crop. This relationship has been also confirmed through calibrated models and data in croplands (Di Falco and Perrings 2003) and in grasslands (Schläpfer et al. 2002). Moreover, other studies (Robinson and Sutherland 2002, Laiolo 2005) investigated the relation between agricultural choices and biodiversity consequences and show that strong agro-diversity has a positive impact on farmland biodiversity. However, no modeling of the economic drivers underlying such an effect has been developed.

The objective of our present paper is to examine the positive economic role played by risk aversion on bird diversity in farmlands. To this end we developed a bio-economic dynamic model is for metropolitan France, spatialized at the regional scale. By comparing the role played by the degrees of farmer risk aversion on bio-economic outcomes, it aims at quantifying the impact of aversion on the agroecosystem for both private (income) and public (farmland birds) goods.

To address such agro-environmental issues, different bio-economic modeling frameworks have been proposed in the literature. Cost–benefit methods require quantification of biodiversity in monetary terms (Drechsler 2001, Rashford et al. 2008). Although pricing techniques such as contingent valuation are available, their suitability for the complex issues of biodiversity is disputed, notably in anthropogenic systems (Diamond and Hausman 1994). In this context, cost effectiveness is an interesting alternative to avoid monetary evaluation of environmental goods (Gatto and De Leo 2000). Approaches such as ecological economics suggest studying environmental and economic performances simultaneously, stressing the relevance of multi-criteria approaches (Drechsler et al. 2007*b*, Mouysset et al. 2011). However, the metrics to adopt for evaluating biodiversity are not self-apparent, and indicators used to assess biodiversity and environmental services are highly diverse (van Wenum et al. 2004, Havlik et al. 2005, Polasky et al. 2005). Moreover, numerous models emphasize spatial dimensions in dealing with agro-ecological issues. Such spatially explicit models aim at assessing consequences of different land-use patterns for various environmental and economic criteria (Irwin and Geoghegan 2001, Polasky et al. 2005, Groot et al. 2009). Nevertheless, most of these models are static, restricting the potential ecological processes accounted for. In the same vein, most models are deterministic and do not take into account the various uncertainties involved in the ecological and economic processes at play.

The bio-economic model proposed in this article is in direct accord with these considerations. It integrates representative rational agents selecting farming land uses in an uncertain economic context through some expected utility and bird community dynamics driven by these land uses. The model is thus dynamic. Furthermore, it articulates ecological and economic compartments and adopts a multi-criteria perspective. It also offers a spatialized perspective as it is built up at a macro-regional scale and its calibration relies on French regional data of both land use and bird abundance. Biodiversity is measured through the European Farmland Bird Index (FBI) which has already shown its relevance to reflect the response of farmland biodiversity to agriculture intensification (Doxa et al. 2010, Mouysset et al. 2011, 2012). Moreover, the model accounts for economic uncertainties through gross margins. In this context, different projections and scenarios at the 2050 horizon give insights into the positive influence of economic risk aversion for reconciling agricultural income and biodiversity. We show how such multi-functionality is related to the heterogeneity of farming habitats and land uses. Thus the major contribution of the paper regards the favorable role of risk aversion as an economic driver for birds biodiversity through the diversity of crops and farming land uses.

The paper is organized as follows: the next section describes the spatialized dynamic model and the bio-economic indicators; the following section presents the results regarding the influence of risk aversion on bio-economic performances; and the final section is devoted to the discussion of these results.

Material and Methods

Context and data

Metropolitan France is split into 620 small agricultural regions (PRA, Petites Regions Agricoles). A PRA is part of a department (a major French administrative entity) which exhibits an agroecological homogeneity. This consistency from both the ecological and economic points of view makes the PRA scale well suited for our bio-economic modeling. The model described below is built for each PRA.

To assess the ecological performance, we here choose to focus on common bird populations and related indicators (Gregory et al. 2004). Although the metric and the characterization of biodiversity remain an open debate (MEA 2005), such a choice is justified for several reasons (Ormerod and Watkinson 2000): (1) birds lie at a high level in the trophic food chains and thus capture variations along the chains; (2) birds provide many ecological services, such as the regulation of rodent populations and pest control, thus justifying our interest in their conservation and viability (Şekercioğlu et al. 2004); and (3) the location of birds close to humans makes them a simple and comprehensive example of biodiversity for a large audience of citizens.

We used the STOC (Suivi Temporal des Oiseaux Commune; French Bird Breeding Survey) database as the source of information related to bird abundances across the whole country (see the Vigie-Nature website).[4] (The data are based on standardized monitoring of spring-breeding birds at 1747 2-km^2 plots across the whole country; details of the monitoring method and sampling design can be found in Jiguet [2009].) Abundance values for each species were available for the period 2001–2008. For each species, we further performed a spatial interpolation of these abundance data to obtain relative abundance values for each possible square in the country (e.g., 136 000 squares [each 2 $\times$ 2 km]) using kriging models based on spatial autocorrelation and the exponential function (Doxa et al. 2010). We then averaged the abundance values at the PRA scale. Among the species monitored by this large-scale long-term survey, we selected 20 species that have been classified as farmland specialists according to their habitat requirements at the European scale (European Bird Census Council 2007). Table 1 lists the 20 species used as a reference for the European Farmland Bird Index FBI (Gregory et al. 2004). Previous analyses have shown the relevance of the national FBI to reflect the response of farmland biodiversity to agricultural intensification and changes (Doxa et al. 2010, Mouysset et al. 2012).

For agro-economic data, we use the French agro-economic classification OTEX (orientation technico-economique) developed by the French Farm Accounting Data Network (FADN, *available online*)[5] of the European Commission and the Observatory of Rural Development (ODR) of the French Institute for Agronomy Research (*available online*).[6] The ODR distinguishes 14 classes of land uses denoted by OTEX (see Table 2). Each PRA is a specific combination of these OTEX land-use classes. The surfaces dedicated to each of the 14 OTEX and the associated gross margins relying on tax return, for the years 2001 to 2008, are available on the ODR website under a private request. "Gross margin" is an economic index broadly used in agricultural economics (see, e.g., Lien 2002).

The ecological model

Regarding bird populations, we chose a dynamic framework. We here adopt the Beverton-Holt model, which accounts for intraspecific competition and density dependence as follows:

$$N_{s,r}(t+1) = N_{s,r}(t)\,\frac{1+R_{s,r}}{1+\dfrac{N_{s,r}(t)}{M_{s,r}(t)}} \qquad (1)$$

where $N_{s,r}(t)$ stands for the bird abundance of species s in a PRA r at year t. The $R_{s,r}$ coefficient corresponds to the intrinsic growth rate specific to each species s in a region r (Smith et al. 2009). This parameter takes into account the characteristics of each species such as clutch size, mean reproductive success, number of clutches per year. The variable $M_{s,r}$ captures the ability of the habitat to host the species, and the product $M_{s,r}(t) \times R_s$ represents the carrying capacity of the habitat r.

The habitat variable $M_{s,r}(t)$ is assumed to depend linearly on land uses (OTEX) as follows:

$$M_{s,r}(t) = \beta_{s,r} + \sum_k \alpha_{s,r,k}\,A_{r,k}(t) \qquad (2)$$

where $A_{r,k}(t)$ represents the share of the PRA r dedicated to OTEX k at time t. The $\alpha_{s,r,k}$ and $\beta_{s,r}$ coefficients, specific to each species, quantify how the species s responds to the various OTEX k in a given region r. The $\beta_{s,r}$ coefficient can be interpreted as the mean habitat coefficient for a species s in a PRA r.

To estimate these different parameters, we use a least-square method to minimize errors between the observed abundances $N^{\text{Data}}_{s,r}$ as issued from STOC survey and the values $N_{s,r}$ computed by the model:

$$\min_{R,\alpha,\beta} \sum_{r,t} \left(N^{\text{Data}}_{s,r}(t) - N_{s,r}(t)\right)^2. \qquad (3)$$

This program determines the parameters R, α, and β of the model, which minimizes the distance between the observed data and the computed data. Fig. 1 illustrates the results of this calibration for national abundances of two species: the Stonechat *Saxicola torquatus* and the Red-backed Shrike *Lanius collurio*. More globally, the mean errors of estimation per PRA are about 0.08%. Comparing the historical abundances with the model-generated ones, we note that the model tends to smooth the variations of the observed data.

The economic model of the farmer

Each PRA r is assumed to be managed by a representative farmer who selects land uses (OTEX) along time. The boundaries of the PRA do not correspond to real management boundaries of individual farmers. However, as the PRA exhibits some agronomic homogeneity, the individual farmers within a PRA face similar environment and constraints. Pooling these farmers into a representative farmer at the PRA scale appears thus as a reasonable hypothesis. The representative farmer determines the surfaces $A_{r,k}(t)$ of each OTEX k in a PRA r in order to maximize some expected utility depending on mean and dispersion of incomes together with risk aversion. The income $\text{Inc}_r(t)$ is the sum of the incomes generated by the agricultural activities k through the unit gross margins $\text{gm}_{r,k}(t)$:

$$\text{Inc}_r(t) = \sum_k \text{gm}_{r,k}(t)\,A_{r,k}(t). \qquad (4)$$

Gross margins $\text{gm}_{r,k}(t)$ are supposed to be uncertain. The variability on gross margins includes market, production, and climate uncertainties. A Gaussian distribution parameterized with the mean and the covariance matrix of the historical data is chosen to

[4] http://www2.mnhn.fr/vigie-nature/
[5] http://ec.europa.eu/agriculture/rica/
[6] https://esrcarto.supagro.inra.fr/intranet/

TABLE 1. List of the 20 farmland bird species used in the model, selected from the French breeding bird survey.

Farmland bird species, *s*		
Species number	Common name	Scientific name
1	Buzzard	*Buteo buteo*
2	Cirl Bunting	*Emberiza cirlus*
3	Corn Bunting	*Emberiza calandra*
4	Grey Partridge	*Perdix perdix*
5	Hoopoe	*Upupa epops*
6	Kestrel	*Falco tinnunculus*
7	Lapwing	*Vanellus vanellus*
8	Linnet	*Carduelis cannabina*
9	Meadow Pipit	*Anthus pratensis*
10	Quail	*Coturnix coturnix*
11	Red-backed Shrike	*Lanius collurio*
12	Red-legged Partridge	*Alectoris rufa*
13	Rook	*Corvus frugilegus*
14	Skylark	*Alauda arvensis*
15	Stonechat	*Saxicola torquatus*
16	Whinchat	*Saxicola rubetra*
17	Whitethroat	*Sylvia communis*
18	Wood Lark	*Lullula arborea*
19	Yellowhammer	*Emberiza citrinella*
20	Yellow Wagtail	*Motacilla flava*

Notes: We selected 20 species that have been classified as farmland specialists according to their habitat requirements at a European scale. These 20 species are used as a reference for the European farmland bird index, FBI (Gregory et al. 2004).

capture such uncertainties. Also assumed is a quadratic form for the utility function of the representative agent (Lien 2002). Even if the mean–variance preference can be criticized (Gollier 2001), it is a convenient function from a modeling viewpoint. Hence, the utility $U_r(t)$ for the representative farmer corresponds to the difference between an expected income $E[\text{Inc}_r(t)]$ and its risky part $\text{Var}[\text{Inc}_r(t)]$:

TABLE 2. List of the 14 classes of farming land uses named OTEX (orientation technico-economique).

The 14 land uses (OTEX)	
Index number, *k*	Definitions
1	cereal, oleaginous, and proteaginous (COP) crops
2	variegated crops
3	intensive bovine livestock breeding
4	medium bovine livestock breeding
5	extensive bovine livestock breeding
6	mixed crop–livestock farming with herbivorous direction
7	other herbivorous livestock breeding
8	mixed crop-livestock farming with granivorous direction
9	mixed crop-livestock farming with other direction
10	granivorous livestock breeding
11	permanent farming
12	flower farming
13	viticulture
14	other associations

Note: OTEX was developed by the French Farm Accounting Data Network (FADN) and the European Union's Observatory of Rural Development (ORD).

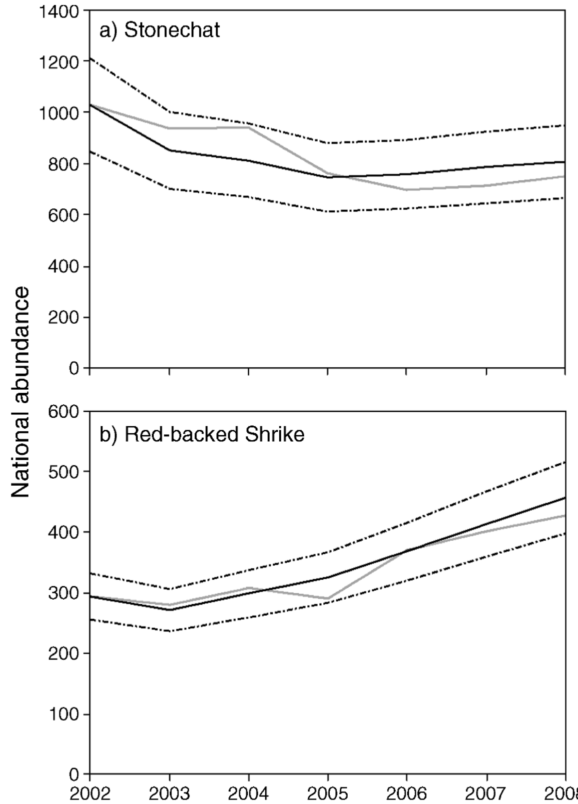

FIG. 1. Comparison between historical (i.e., observed) $N_{s,r}(t)$ (gray curve) and estimated (i.e., computed) $\hat{N}_{s,r}(t)$ (black curve) national abundances in France together with the least-squares standard errors of calibration at 95% (dashed lines), for two of the species considered: (a) the Stonechat *Saxicola torquatus* and (b) the Red-backed Shrike *Lanius collurio*.

$$U_r(t) = E[\text{Inc}_r(t)] - a.\text{V}ar[\text{Inc}_r(t)] \quad (5)$$

$$= \sum_k \overline{\text{gm}}_{r,k}.A_{r,k} - a \sum_k \sum_{k'} \sigma_{r,k'}(t)\, A_{r,k}(t)\, A_{r,k'}(t). \quad (6)$$

Expected gross margins $\overline{\text{gm}}_{r,k}$ are the mean of the seven historical years, i.e., $\overline{\text{gm}}_{r,k} = \frac{1}{7}\sum_{t=1}^{t=7} \text{gm}_{r,k}(t)$.

The coefficient a represents the risk-aversion level of the farmer: the higher the a, more risk averse the farmer. In particular $a = 0$ means farmers are risk neutral, they make their choices only focusing on the expected income. The risky term is computed with the covariance $\sigma_{r,k,k'}$ between margins of land-uses k and k' in region r, i.e., $\sigma_{r,k,k'} = \frac{1}{7}\sum_{t=1}^{t=7}\left[\text{gm}_{r,k}(t) - \overline{\text{gm}}_{r,k}(t)\right]\left[gm_{r,k'}(t) - \overline{\text{gm}}_{r,k'}(t)\right]$.
The maximizing program of farmer's utility in an uncertain context is defined as follows:

$$\max_{A_{r,1};\ldots;A_{r,14}} U_r(t). \quad (7)$$

Furthermore, when maximizing the utility, the standard agent must comply with two constraints at every point in

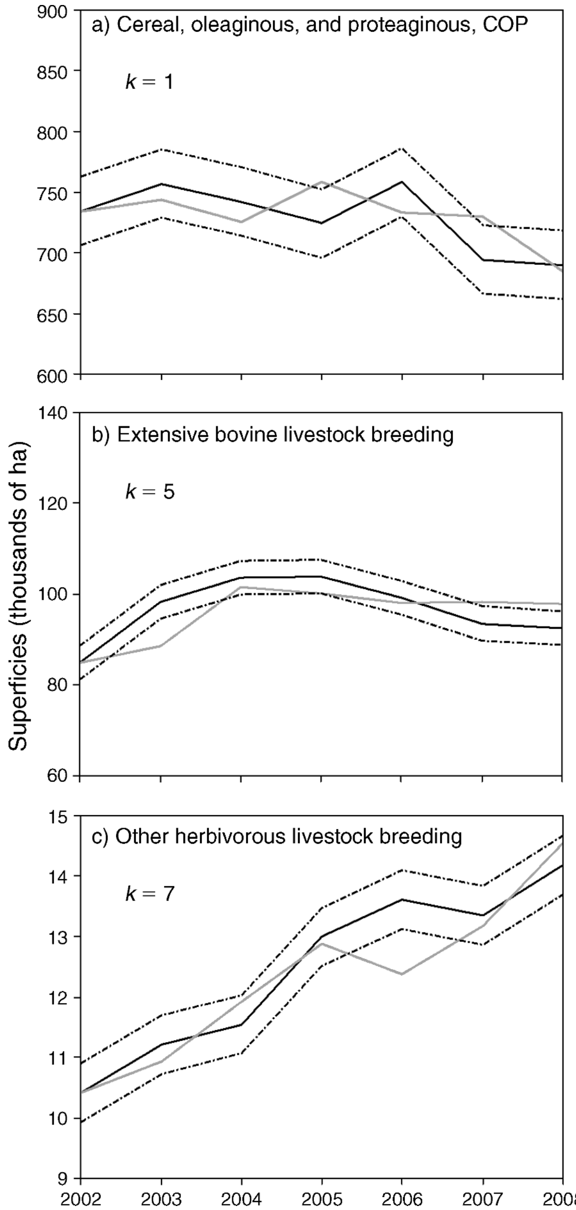

FIG. 2. Three examples at the PRA (Petites Regions Agricoles) scale of comparison between historical (observed) $A_{r,k}(t)$ (gray lines) and estimated (computed) $\hat{A}_{.,k}(t)$ (black lines) land-use areas; "*A*" is area, and "*k*" is the OTEX land-use classification number (see Table 2). The dashed lines are the least-squares standard errors of calibration at 99%.

time:

$$|A_{r,k}(t) - A_{r,k}(t-1)| \leq \varepsilon A_{r,k}(t-1) \tag{8}$$

$$\sum_k A_{r,k}(t) = A_r. \tag{9}$$

The first constraint (Eq. 8) corresponds to a technical constraint where the coefficient ε stands for the rigidity in changes. For example, the case where $\varepsilon = 0$ means that the land uses remain constant. The second constraint (Eq. 9) merely ensures that the total agricultural surface A_r per PRA remains constant. Typically, forest and urban areas are assumed to be steady.

To estimate the parameters a and ε, we use a least-square method to minimize errors between the observed superficies $A^{\text{Data}}_{r,k}(t)$ dedicated to each OTEX as issued from the databases and the values derived from the model $A_{r,k}(t)$:

$$\min_{a,\varepsilon} \sum_{r,k,t} [A^{\text{Data}}_{r,k}(t) - A_{r,k}(t)]^2. \tag{10}$$

Similarly to the ecological model, this program lets us determine the parameters a, ε of the economic model, which minimizes the errors between the observed and computed superficies. Fig. 2 illustrates the results of this calibration for three examples of superficies at the PRA scale: the COP (OTEX 1 in Table 2), the Extensive bovine livestock breeding (OTEX 5 in Table 2) and the Other herbivorous livestock breeding (OTEX 7 in Table 2). More globally, the average error of estimation at the national scale is about 1.3% per hectare. The calibration leads to $\varepsilon = 10\%$ and $a = 10^{-7}$.

Projections and indicators

Ecological and economic models described previously are thus linked through the agricultural system's OTEX as depicted by Fig. 3. With the objective of maximizing incomes under technical and inertia constraints, the representative farmer in each PRA selects a pattern of OTEX $A_{r,k}(t)$ which impacts the ecological dynamics through the habitat $M_{s,r}(t)$. The farming land uses are outputs of the economic model and inputs of the ecological model. The economic

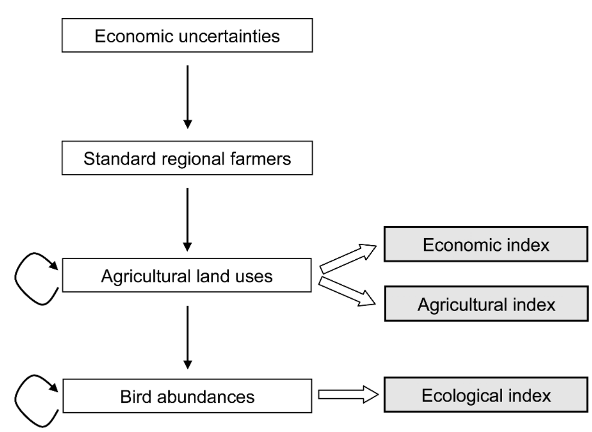

FIG. 3. Schematic depiction of model coupling (the coupling between ecological and economic models; see *Material and methods*). Farmers maximize their utility function and adjust their land uses depending on economic uncertainty and their risk aversion. These choices affect bird community dynamics.

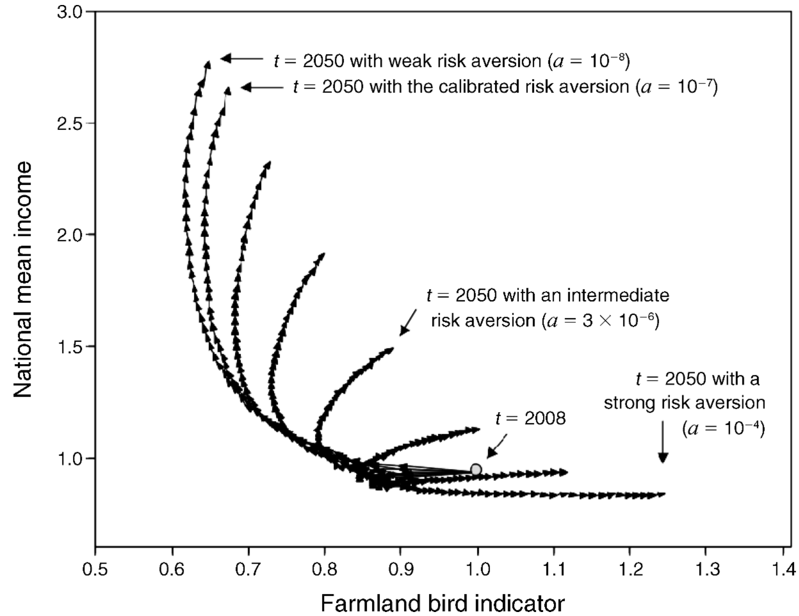

FIG. 4. Mean bio-economic performances and trade-off between national mean income, $\overline{\mathrm{Inc}}_{\mathrm{nat}}(t)$, and the Farmland Bird Index, $\mathrm{FBI}_{\mathrm{nat}}(t)$, in a context of economic uncertainty for different levels of risk aversion, a. All trajectories start at the same solid gray circle: $t = 2008$ (see *Material and methods*).

choices thus condition bird abundances $N_{s,r}(t)$ associated with the habitats.

We made different projections to analyze possible future trends of agriculture and biodiversity according to the risk aversion of farmers involved in utility as defined in Eq. 6. We tested eight absolute risk-aversion levels a between 10^{-4} and 10^{-8} as suggested by Lien (2002) in a similar economic context. For the projections we do not add public policies, in contrast to Mouysset et al. (2011). In other words, the case studied here corresponds to a status quo scenario in the sense that it is assumed that the farmers evolve under the current policy context. To focus on the effect of the only aversion parameter, we consider the farmers as "price takers" since their choices do not temporally affect the gross margins. The selected time frame runs from 2009 to 2050, i.e., a 42-year forecast. Selecting a shorter time frame could consequently hide interesting long-term effects due to the inertia of the models.

To analyze bio-economic performances, we focus on ecological effects, land-use choices, and economic performances at national and regional scales.

Biodiversity index

From an ecological viewpoint, we have selected the Farmland Bird Index (FBI). We focus on this indicator, which has been adopted by the European Community as the official environmental index especially to analyze structural changes in biodiversity (Balmford et al. 2003). FBI is an index of variation in abundances here computed with respect to the reference year 2008. We first estimated a regional FBI with 20 farmland specialist species (Table 1) for each PRA r as follows:

$$\mathrm{FBI}_r(t) = \prod_{s \in \mathrm{Specialist}} \left(\frac{N_{s,r}(t)}{N_{s,r}(2008)} \right)^{1/20}. \quad (11)$$

Then at the national scale for France we considered the aggregated indicator $\mathrm{FBI}_{\mathrm{nat}}$:

$$\mathrm{FBI}_{\mathrm{nat}}(t) = \prod_{s \in \mathrm{Specialist}} \left(\frac{N_{s,\mathrm{nat}}(t)}{N_{s,\mathrm{nat}}(2008)} \right)^{1/20} \quad (12)$$

where $N_{s,\mathrm{nat}}(t)$ stands for the total abundance of species s over all PRA r.

Economic index

From an economic viewpoint, we use the regional income. $\mathrm{Inc}_r(t)$ defined in Eq. 4 and the national mean income per hectare $\overline{\mathrm{Inc}}_{\mathrm{nat}}(t)$ defined in Eq. 13. The national income is computed from the mean gross margin of the 620 PRA:

$$\overline{\mathrm{Inc}}_{\mathrm{nat}}(t) = \frac{1}{A_{\mathrm{nat}}} \sum_{r=1}^{620} A_r \mathrm{Inc}_r(t) \quad (13)$$

where $A_{\mathrm{nat}} = \sum_{r=1}^{620} A_r$ is the total surface of PRA over France. For the sake of clarity, we will represent this criterion on Figs. 4 and 5 after a normalization by their current value (2008).

Habitat heterogeneity index

To analyze farming habitat heterogeneity, we use a habitat heterogeity index denoted by $\mathrm{Hdiv}_r(t)$, which

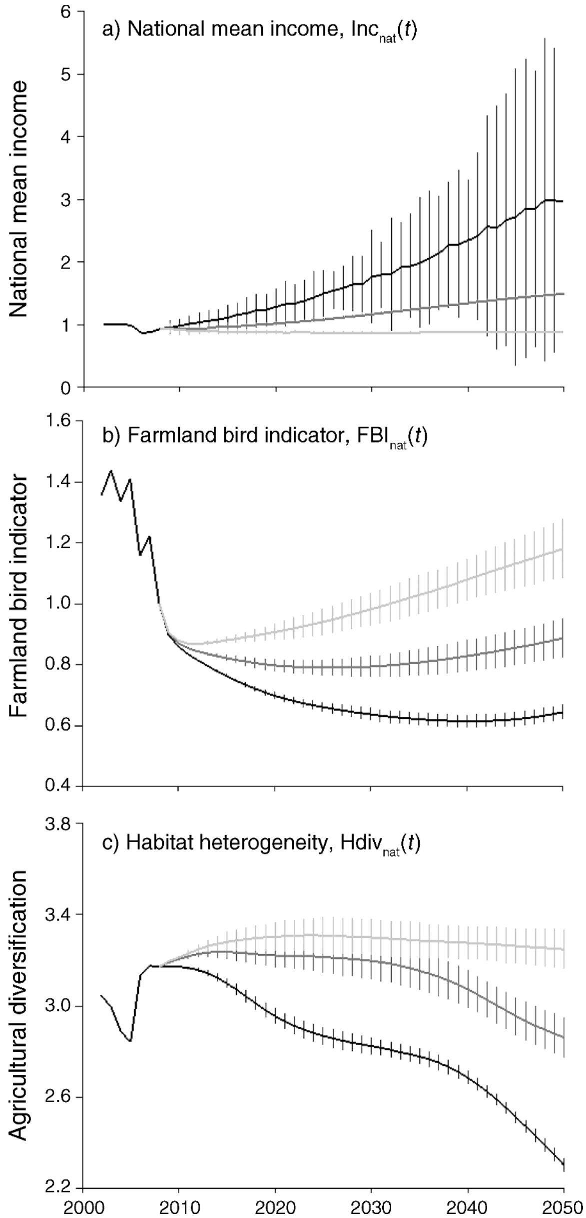

FIG. 5. Bio-economic performance and habitat heterogeneity up to 2050 for three contrasted risk-aversion levels, together with 99% confidence intervals: black, weak risk aversion; medium gray, intermediate risk aversion; light gray, strong risk aversion; black left of 2009, historical data). [As these data were (a) normalized, (b) a variation related to 2008, or (c) a proportional index, there are no units.]

corresponds to an agricultural diversification index. In the same vein as Di Falco and Perrings (2003), it is here computed as the Simpson index of land uses $A_{r,k}(t)$:

$$\text{Hdiv}_r(t) = \left(\sum_{k=1}^{14}\left[\frac{A_{r,k}(t)}{A_r(t)}\right]^2\right)^{-1}. \quad (14)$$

This indicator evaluates the bias compared to the equi-distribution. Its maximum is achieved when the agricultural area is divided equally among the 14 OTEX.

We also estimate an average heterogeneity indicator over France, $\text{Hdiv}_{\text{nat}}(t)$, as an arithmetic mean of the 620 indicators at the PRA scale:

$$\text{Hdiv}_{\text{nat}}(t) = \frac{1}{620}\sum_{r=1}^{620}\text{Hdiv}_r(t). \quad (15)$$

RESULTS

As the modeling is realized in an uncertain context, we run one hundred simulations with different random Gaussian gross margins $\text{gm}_{r,k}(t)$ from $t = 2009$ to $T = 2050$. Then both at PRA and national scales, we compute at any time the mean of the simulations for ecological, economic, and habitat heterogeneity indices $\text{FBI}(t)$, $\text{Inc}(t)$, and $\text{Hdiv}(t)$ along with their 99% confidence intervals.

Bioeconomic performances depending on risk aversion

We first compare the bio-economic performances $\text{FBI}(t)$ (farmland bird index at time t) and $\text{Inc}(t)$ (income at time t) for the various levels of risk aversion at the national scale. Fig. 4 represents the mean of the 100 simulations for different risk aversion a. We observe a set of contrasted trajectories: Those with strong risk-aversion levels are beneficial to biodiversity while those with weak risk-aversion levels promote the economic indicator. In other words, risk aversion plays a significant role in the bio-economic performances achieved over time. However the ecological and economic performances are negatively correlated, and thus different trade-offs can occur: there is no path optimizing both the economic and the biodiversity criteria.

Performances and volatilities

Fig. 5 compares the national bio-economic performances and agricultural diversification by displaying the means with 99% confident interval for three contrasted levels of risk aversion a. We observe a positive correlation between FBI and agricultural diversification. This is clearly confirmed by a statistical analysis ($R^2 = 57\%$, $P \leq 2.2 \times 10^{-16}$): positive ecological performances are associated with the stronger habitat heterogeneity index.

Concerning the dispersion of the outputs, the national income is the most stongly affected indicator. The lowest risk aversion allows for a better growth of national income in the mean but with the largest deviation. By contrast, with the strongest risk aversion, the national income is just stabilized but the volatility vanishes. The intermediate risk aversion leads to a moderate income growth with reduced volatility. On the ecological side, we note that economic risk aversion does not strongly affect the dispersion of farmland bird indicators. The standard deviation is about 3% for all cases. Similarly the habitat heterogeneity index dispersion is not deeply impacted by risk aversion as it ranges from 2% to 3%.

Performances at the PRA scale

Fig. 6 displays the habitat diversification indicator $\text{Hdiv}_r(t)$ at the PRA scale—the scale of the 620 small agricultural regions (Petites Regions Agricoles) into which all of France is divided—in 2008 ($t = 0$) and in 2050, with three contrasted risk strategies. Risk aversion plays qualitatively the same role for the broad majority of regions. With strong risk aversion, habitat heterogeneity occurs. Conversely, with weak risk aversion we observe a specialization for most regions: the heterogeneity index decreases in comparison with 2008.

Fig. 7 compares the $\text{FBI}_r(t)$ at the PRA scale in 2008 and in 2050 for the three risk-aversion levels a. It turns out that the effect of risk aversion on ecological performances at the PRA scale is more reduced than on the agricultural heterogeneity. We observe a global enhancement of regional FBI for the strongest risk-aversion levels. Still, contrary to the habitat heterogeneity maps of Fig. 6, Fig. 7 captures many regional differences: some PRA have a significant FBI improvement and others exhibit a steady FBI.

Statistical analysis strongly emphasizes significant correlations between habitat heterogeneity index and FBI for all PRA ($P \leq 2.2 \times 10^{-16}$). Nevertheless the quality of the fitness varies among the PRA: R^2 varies between 3% and 94%, with a mean at 20%.

Finally, Fig. 8 compares the mean income $\text{Inc}_r(t)$ at the PRA scale in 2008 and in 2050 for the three levels of risk aversion. Although risk aversion globally lessens the incomes, many regional discrepancies emerge, similar to bird biodiversity.

Discussion

Spatiotemporal bio-economic models to manage biodiversity

This paper presents an interdisciplinary approach which is needed (Polasky et al. 2005, Perrings et al. 2006, Mouysset et al. 2011) to effectuate a sustainable management of biodiversity and agriculture. Despite divergences between economic and ecological disciplines (Drechsler et al. 2007*a*), our model couples economic and ecological dynamics to analyze bio-economic performances of French agriculture at the national scale. This approach avoids the monetary evaluation of biodiversity, which is controversial. The coupling of ecological (bird abundances), land-use, and economic (gross margins) data gives strong realism to the modeling. The precision to integrate these data compensates for the simple formalism of the model and makes it possible to obtain robust and informative results. With the account of regional economic and ecological specificities, the model is spatialized at the landscape level, which reinforces its relevance (Polasky et al. 2005). Taking account of economic uncertainties through gross margins also reinforces its credibility. As compared to Mouysset et al. (2011, 2012), the introduction of such a stochasticity constitutes a major methodological novelty. The choice to focus on common birds rather than one or two emblematic species makes it possible to obtain more general results regarding biodiversity. Finally, the explicit and mechanistic modeling of the ecological process (with intraspecific competition) and its dynamic perspective (with an adjustment of the carrying-capacity function of land uses) lead to a precise representation of the impact of land uses on avifauna changes and transient dynamics. The integration of these uncertain spatiotemporal components, multi-scale data, and the multi-criteria viewpoint creates a flexible modeling framework allowing for many developments and refinements.

Risk aversion to reconcile biodiversity and economic scores

Some studies have already stressed the positive impact of genetic diversity (i.e., agro-biodiversity) on the management of economic risk. In this perspective, Schläpfer et al. (2002) for grasslands, Di Falco and Perrings (2003) and Di Falco et al. (2007) for croplands, or Baumgärtner and Quaas (2010) in a theorical approach need to be mentioned. Although keeping a similar viewpoint, the present study suggests a more general mechanism based on the global diversification of the land uses: thanks to a portfolio effect, risk-averse farmers diversify their agricultural activities in order to dampen the uncertainties on expected incomes and manage their economic risk. With these insurance effects, the diversification has a positive effect on private goods (income).

Moreover this diversification also has a strong positive impact on the production of public goods (biodiversity). Indeed, agricultural diversification creates heterogeneity of habitats and available resources, both of which are essential for birds, as stressed by Benton et al. (2003). This positive effect of diversification on biodiversity has been experimentally and separately identified for different land uses in Laiolo (2005) for crop landscapes and in Robinson and Sutherland (2002) for grasslands. A strong risk-averse behavior leads to a simultaneous land-use diversity, which improves the dynamics of bird communities.

Indeed, the diversity of land uses leads to a coexistence of different kinds of farmland habitat. Farmland species with different habitat requirements, such as cropland birds (e.g., Skylark *Alauda arvensis*, Grey Partridge *Perdix perdix*) or grassland birds (e.g., Meadow Pipit *Anthus pratensis*, Whinchat *Saxicola rubetra*), are thus able to coexist at the scale of the PRA. By offering more diverse farmed habitats the total number of birds is increased. This conclusion is also interesting in the context of the current ongoing biotic homogenization (McKinney and Lockwood 1999, Olden 2006) that has been identified as a major issue in

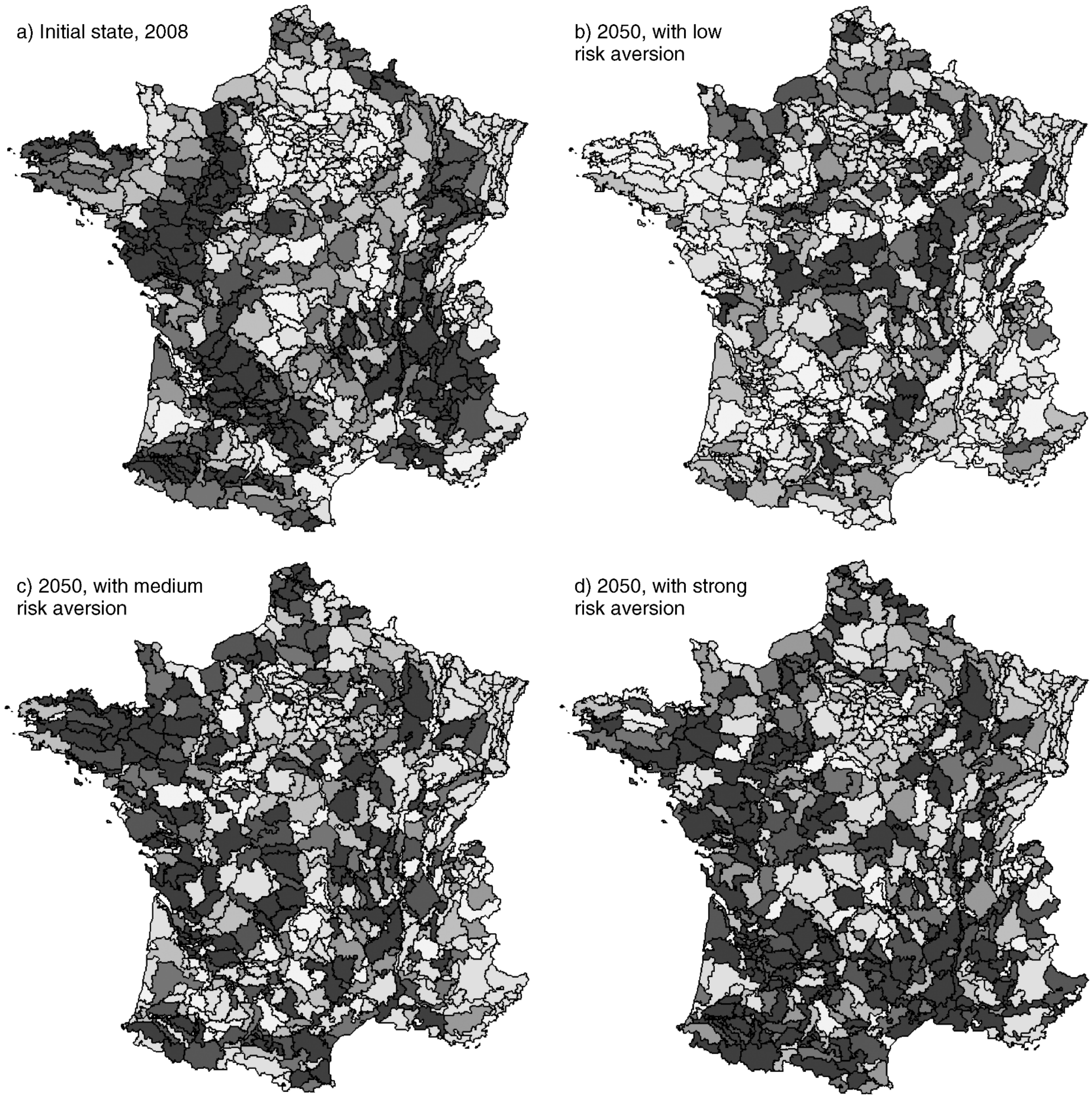

FIG. 6. Comparison of habitat heterogeneity index, $Hdiv_r(t)$, at the PRA scale in 2008 and in 2050 according to the risk-aversion level (darker grays, strong diversity; paler grays, weak diversity; white, data not available). A color version of this figure is available in the Appendix: Fig. A1.

farmlands. This biotic homogenization, characterized by a replacement of specialist species by more generalist species (Devictor et al. 2008), is often a consequence of strong declines of habitat specialists (Julliard et al., 2004). Previous studies suggested diversifying agricultural practices to counter this homogenization (Doxa et al. 2012); we highlight here the diversification of land use as another lever to stimulate the development of farmland specialists and limit biotic homogenization in farmlands.

Land-use heterogeneity induced by risk-averse farmers thus seems an efficient way of promoting both private and public values. The main contribution of our paper is to derive such an effect for biodiversity at a large spatial scale (620 PRA over France) and for a large number of species through common birds (20 species). More globally, farming diversification is positive for the functioning of the agroecosystem. According to the insurance hypothesis (Yachi and Loreau 1999), an increasing biodiversity insures ecosystems against declines in their functioning caused by environmental fluctuations. Such an effect is expected because different species can adapt differently to environmental changes (Doak et al. 1998, Ives et al. 1999). Communities with strong biodiversity are more stable and more productive in the ecological sense than those with poor biological

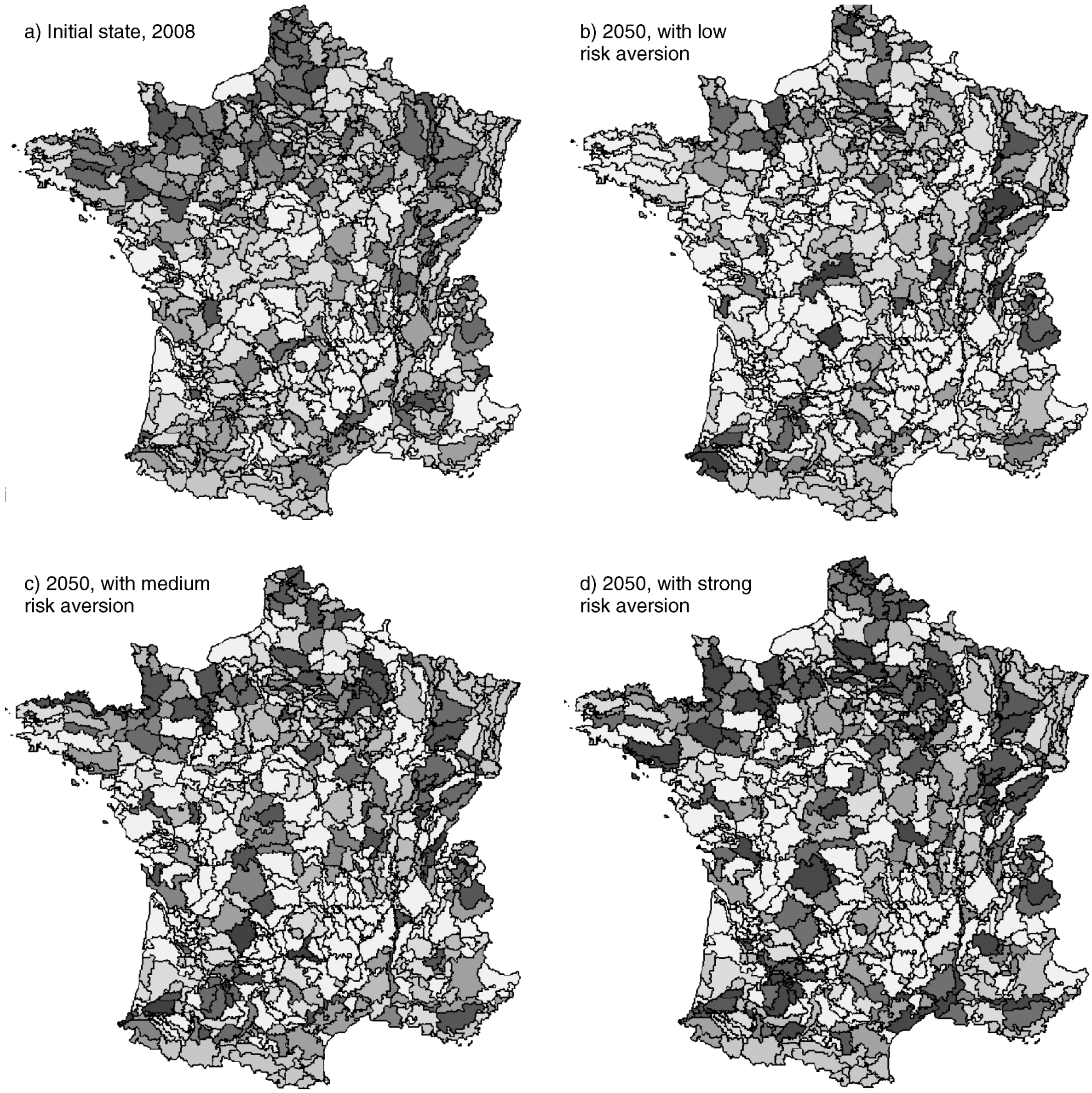

FIG. 7. Comparison of Farmland Bird Index, $FBI_r(t)$, at the PRA scale in 2008 and in 2050, according to the risk-aversion level (darker grays, strong FBI; paler grays, weak FBI; white, data not available). A color version of this figure is available in the Appendix: Fig. A2.

diversity (Caldeira et al. 2005). Hence, agricultural habitat diversity acts as a public natural insurance. Moreover, a larger and more diverse community provides the agrosystems with various ecosystem services such as pest control, pollination, and decomposition processes (Altieri 1999, Schläpfer et al. 1999, Tilman et al. 2002), and consequently induces stronger ecosystem viability. These services should indirectly contribute to farming production and to its sustainability. In this context, agricultural diversification developed by risk-averse farmers could itself be identified as an ecosystem service yielding both private and public insurance effects for the agroecosystem.

Confrontation to the current biodiversity decline

This study suggests that biodiversity management and conservation are positively affected by economic risk aversion. This aversion seems sufficient for the farmers to select their land uses in an eco-friendly manner. Consequently the result presented here, based on utility maximization without any ecological awareness or goals, has sound connections with the theoretical statement of Quaas et al. (2007) that farmers do not necessarily need to have environmental preferences or to receive monetary benefits from ecosystem services to favor a land-use strategy allowing for a sustainable path for biodiversity. While the economic agents are generally

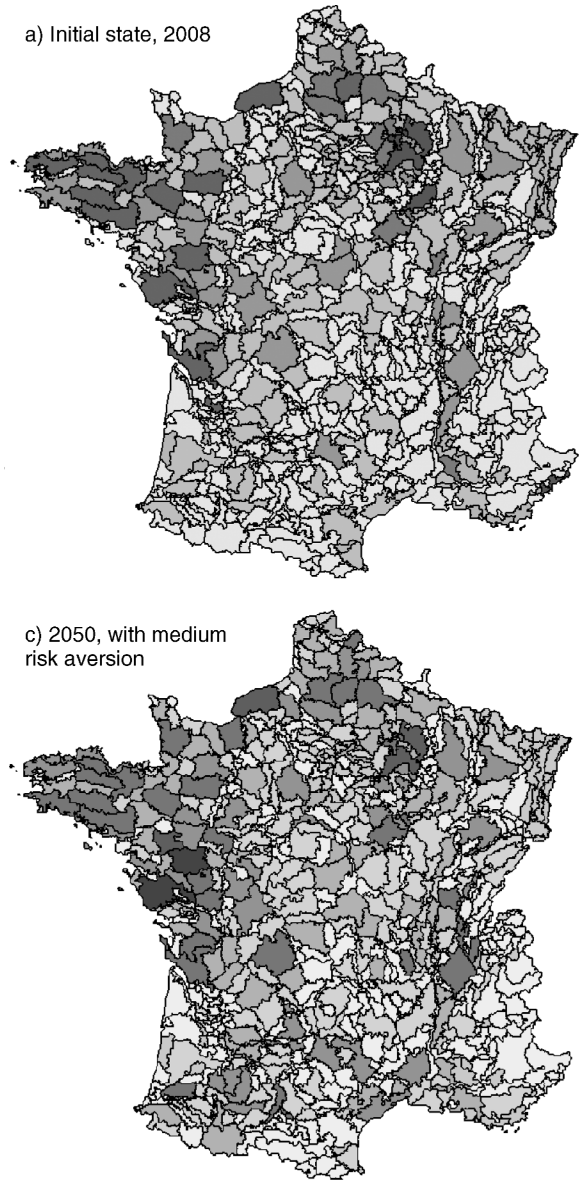

FIG. 8. Comparison of income, $Inc_r(t)$, at the PRA scale in 2008 and in 2050 according to the risk-aversion level (darker grays, strong income; paler grays, weak income; white, data not available). A color version of this figure is available in the Appendix: Fig. A3.

considered risk averse, our calibration leads to a weak risk-aversion parameter. This conclusion is consistent with the current decline of farmland birds. Two hypotheses could explain this weak risk aversion. First, the agricultural economics was very protected by the Common Agricultural Policy. This policy has been built to protect farmers against market volatilities and price fluctuations by distributing economic compensations. In this context, in spite of risk-averse behavior, farmers are encouraged to specialize their activities (as observed with risk-neutral behavior), which has a negative impact on farmland birds. The second hypothesis concerns the financial insurance. To limit the economic risk, the risk-averse farmers can opt for either natural insurance (i.e., agricultural diversification of land uses and genetic varieties) or financial insurance specific to a specialized activity (Quaas and Baumgärtner 2008). This monetary insurance has shown detrimental effects for ecological performances by promoting more risky production (Horowitz and Lichtenberg 1993, Mahul 2001).

Strong spatial disparities

The previous conclusions at the national scale are intuitive and consistent with the literature. However another important contribution of this study is to provide a multi-scale analysis and complete the usual approach with a spatial viewpoint of regional scores. This spatial distribution highlights an interesting effect: trends at the national scale hide many disparities between local regions (here PRA). Economic risk aversion is sufficient to globally promote biodiversity at the national scale, but it is not enough for every PRA. Hence, some regions that enhance agricultural heterogeneity in a context of strong risk aversion do not always exhibit a strong FBI. This result suggests that other mechanisms influence bird dynamics. In particular, the quality of the diversification could be important: some agricultural systems such as extensive farming are decisive for specific bird populations. In this context, public policies could be developed to favor some agricultural systems and reinforce the diversification mechanisms mentioned above. Strong income differences between PRA are also in favor of public policies to reduce economic disparities. Alavalapati et al. (2002), Shi and Gill (2005), and Mouysset et al. (2011) have shown the effectiveness of some public policies for both ecological and economic criteria. In a regional perspective, the public policies seem to be essential to manage biodiversity and mitigate economic regional differences.

Conclusion

The present modeling work shows how risk aversion directly entails agricultural diversification, which has positive bio-economic impacts for the agroecosystem. The diversification plays on economic performances by mitigating income volatility and potentially by promoting numerous and stable ecosystem services that can be used by the farmers. From the ecological point of view, it promotes biodiversity through broader and stabilized farmland bird communities. This favorable effect of risk aversion as an economic driver for bird diversity constitutes the main novelty of the present work.

However, the bio-economic scenarios suggest that the effect of this risk aversion differs among the PRA. In this context, public incentives could play a fruitful role to reduce both ecological and economic regional disparities. To improve their effectiveness, such policies should account for risk aversion to foster spontaneous diversification. The reinforcement of the present work regarding biodiversity analysis could include further biodiversity metrics, taxa and functional groups. More globally, we are convinced of the interest of developing a multi-criteria approach for biodiversity management from both economic and ecological viewpoints.

Acknowledgments

This work was carried out with the financial support of the ANR (Agence Nationale de la Recherche)—the French National Research Agency—under the "Systerra program–Ecosystems and Sustainable Development," project "ANR-08-STRA-007, FARMBIRD–Coviabilty models of Farming and Bird biodiversity." Such studies would not be feasible without the dedicated help of hundreds of volunteers monitoring the bird communities across the country every year.

Literature Cited

Alavalapati, J. R. R., G. A. Stainback, and D. R. Carter. 2002. Restoration of the longleaf pine ecosystem on private lands in the US South: an ecological economic analysis. Ecological Economics 40(3):411–419.

Altieri, M. A. 1999. The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems and Environment 74(1–3):19–31.

Balmford, A., R. E. Green, and M. Jenkins. 2003. Measuring the changing state of nature. Trends in Ecology and Evolution 18(7):326–330.

Baumgärtner, S., and M. F. Quaas. 2010. Managing increasing environmental risks through agrobiodiversity and agrienvironmental policies. Agricultural Economics 41(5):483–496.

Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003. Farmland biodiversity: Is habitat heterogeneity the key? Trends in Ecology and Evolution 18(4):182–188.

Butler, S. J., D. Brooks, R. E. Feber, J. Storkey, J. A. Vickery, and K. Norris. 2009. A cross-taxonomic index for quantifying the health of farmland biodiversity. Journal of Applied Ecology 46:1154–1162.

Caldeira, M. C., A. Hector, M. Loreau, and J. S. Pereira. 2005. Species richness, temporal variability and resistance of biomass production in a Mediterranean grassland. Oikos 110:115–123.

Chamberlain, D. E., R. J. Fuller, R. G. H. Bunce, J. C. Duckworth, and M. Shrubb. 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. Journal of Applied Ecology 37(5):771–788.

Devictor, V., R. Julliard, J. Clavel, F. Jiguet, A. Lee, and D. Couvet. 2008. Functional biotic homogenization of bird communities in disturbed landscapes. Global Ecology and Biogeography 17(2):252–261.

Diamond, P. A., and J. A. Hausman. 1994. Contingent valuation: Is some number better than no number? Journal of Economic Perspectives 8(4):45–64.

Di Falco, S., J. Chavas, and M. Smale. 2007. Farmer management of production risk on degraded lands: the role of wheat variety diversity in the Tigray region, Ethiopia. Agricultural Economics 36(2):147–156.

Di Falco, S., and C. Perrings. 2003. Crop genetic diversity, productivity and stability of agroecosystems. A theoretical and empirical investigation. Scottish Journal of Political Economy 50(2):207–216.

Doak, D. F., D. Bigger, E. K. Harding, M. A. Harvier, R. E. O Malley, and D. Thomson. 1998. The statistical inevitability of stability-diversity relationship in community ecology. American Naturalist 151(3):264–276.

Doherty, P. F., Jr., E. A. Marschall, and T. C. Grubb, Jr. 1999. Balancing conservation and economic gain: A dynamic programming approach. Ecological Economics 29(3):349–358.

Donald, P. F., R. E. Green, and M. F. Heath. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proceedings of the Royal Society of London B 268(1462):25–30.

Doxa, A., Y. Bas, M.-L. Paracchini, P. Pointereau, J.-M. Terres, and F. Jiguet. 2010. Low-intensity agriculture increases farmland bird abundances in France. Journal of Applied Ecology 47(6):1348–1356.

Doxa, A., M. L. Paracchini, P. Pointereau, V. Devictor, and F. Jiguet. 2012. Preventing biotic homogenization of farmland bird communities: the role of High Nature Value farmland. Agriculture, Ecosystems and Environment 148:83–88.

Drechsler, M. 2001. The importance of economic costs in the development of guidelines for spatial conservation management. Biological Conservation 97(1):51–59.

Drechsler, M., V. Grimm, J. Mysiak, and F. Watzold. 2007*b*. Differences and similarities between ecological and economic models for biodiversity conservation. Ecological Economics 62(2):232–241.

Drechsler, M., F. Watzold, K. Johst, H. Bergmann, and J. Settele. 2007*a*. A model-based approach for designing cost-effective compensation payments for conservation of endangered species in real landscapes. Biological Conservation 140(1–2):174–186.

European Bird Census Council. 2007. State of Europe's common birds 2007. A PECBMS report. Czech Statistical Office and Royal Society of Bird Protection, Prague, Czech Republic. http://www.ebcc.info/

Gatto, M., and G. A. De Leo. 2000. Pricing biodiversity and ecosystem services: The never-ending story. BioScience 50(2):347–355.

Gollier, C. 2001. The economics of risk and time. MIT Press, Cambridge, Massachusetts, USA.

Gregory, R. D., G. D., Noble, and J. Custance. 2004. The state of play of farmland birds: population trends and conservation status of lowland farmland birds in the United Kingdom. Ibis 146(Suppl. 2):1–13.

Groot, J. C. J., W. A. H. Rossing, M. Tichit, N. Turpin, A. Jellema, J. Baudry, P. H. Verburg, L. Doyen, and G. W. J. van de Ven. 2009. On the contribution of modelling to multifunctional agriculture: learning from comparisons. Journal of Environmental Management 90(Suppl. 2):147–160.

Hardaker, J. B. 2000. Some issues in dealing with risk in agriculture. Working Paper number 2000-3. Series in Agricultural and Resource Economics. University of New England, Armidale, New South Wales, Australia.

Havlik, P., P. Veysset, J. M. Boisson, M. Lherm, and F. Jacquet. 2005. Joint production under uncertainty and multifunctionality of agriculture: policy considerations and applied analysis. European Review of Agrigultural Economics 32(4):489–515.

Holzkamper, A., and R. Seppelt. 2007. Evaluating cost-effectiveness of conservation management actions in an agricultural landscape on a regional scale. Biological Conservation 136(1):117–127.

Horowitz, J. K., and E. Lichtenberg. 1993. Insurance, moral hazard, and chemical use in agriculture. American Journal of Agricultural Economics 75(4):926–935.

Irwin, E. G., and J. Geoghegan. 2001. Theory, data, methods: developing spatially explicit economic models of land use change. Agriculture, Ecosystems and Environment 85(1–3):7–24.

Ives, A. R., K. Gross, and J. L. Klug. 1999. Stability and variability in competitive communities. Science 286(5439):542–544.

Jiguet, F. 2009. Method-learning caused first-time observer effect in a newly-started breeding bird survey. Bird Study 56(2):253–258.

Julliard, R., F. Jiguet, and F. Covet. 2004. Common birds facing global changes: What makes a species at risk? Global Change Biology 10(1):148–154.

Kleijn, D., et al. 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecology Letters 9:243–256.

Krebs, J. R., J. D. Wilson, R. B. Bradbury, and G. M. Siriwardena. 1999. A second silent spring? Nature 400:611–612.

Laiolo, P. 2005. Spatial and seasonal patterns of bird communities on italian agroecosystems. Conservation Biology 19:1547–1556.

Lien, G. 2002. Non-parametric estimation of decision makers' risk aversion. Agricultural Economics 27(1):75–83.

Mahul, O. 2001. Optimal insurance against climatic experience. American Journal of Agricultural Economics 83(3):593–604.

McKinney, M., and J. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology and Evolution 14:450–453.

MEA [Millenium Ecosystem Assessment]. 2005. Cultivated systems. Chapter 26 *in* Ecosystems and human well being. Volume 1. Current state and trends. Island Press, Washington, D.C., USA.

Mouysset, L., L. Doyen, and F. Jiguet. 2012. Different policy scenarios to promote various targets of biodiversity. Ecological Indicators 14(1):209–221.

Mouysset, L., L. Doyen, F. Jiguet, G. Allaire, and F. Leger. 2011. Bio economic modeling for a sustainable management of biodiversity in agricultural lands. Ecological Economics 70(4):617–626.

Olden, J. D. 2006. Biotic homogenization: a new research agenda for conservation biogeography. Journal of Biogeography 33(12):2027–2039.

Ormerod, S. J., and A. R. Watkinson. 2000. Editors' introduction: birds and agriculture. Journal of Applied Ecology 37(5):699–705.

Pacini, C., A. Wossink, G. Giesen, and R. Huirne. 2004. Ecological–economic modelling to support multi-objective policy making: a farming systems approach implemented for Tuscany. Agriculture, Ecosystems and Environment 102(3):349–364.

Perrings, C., L. Jackson, K. Bawa, L. Brussaard, S. Brush, T. Gavin, R. Papa, U. Pascual, and P. De Ruiter. 2006. Biodiversity in agricultural landscapes: saving natural capital without losing interest. Conservation Biology 20(2):263–264.

Polasky, S., E. Nelson, E. Lonsdorf, P. Fackler, and A. Starfield. 2005. Conserving species in a working landscape: land use with biological and economic objectives. Ecological Applications 15:1387–1401.

Quaas, M. F., and S. Baumgärtner. 2008. Natural vs. financial insurance in the management of public-good ecosystems. Ecological Economics 65(2):397–406.

Quaas, M., S. Baumgartner, C. Becker, K. Frank, and B. Muller. 2007. Uncertainty and sustainability in the management of rangelands. Ecological Economics 62(2):251–266.

Rashford, B. S., B. D. Dugger, and R. M. Adams. 2008. Application of a bioeconomic production model to improve wildlife management. Journal of Wildlife Management 72:510–517.

Robinson, R. A., and W. J. Sutherland. 2002. Post-war changes in arable farming and biodiversity in Great Britain. Journal of Applied Ecology 39(1):157–176.

Schläpfer, F., B. Schmid, and I. Seidl. 1999. Expert estimates about effects of biodiversity on ecosystem processes and services. Oikos 84(2):346–352.

Schläpfer, F., M. Tucker, and I. Seidl. 2002. Returns from hay cultivation in fertilized low diversity and non-fertilized high diversity grassland. Environmental and Resource Economics 21:89–100.

Şekercioğlu, C. H. Daly, and P. R. Ehrlich. 2004. Economic consequences of bird declines. Proceedings of the National Academy of Sciences USA 101(52):18042–18047.

Shi, T., and R. Gill. 2005. Developing effective policies for the sustainable development of ecological agriculture in China: the case study of Jinshan County with a systems dynamics model. Ecological Economics 53(2):223–246.

Smith, J. R., P. Fong, and R. F. Ambrose. 2009. Spatial patterns in recruitment and growth of the mussel *Mytilus californianus* (Conrad) in southern and northern California, USA, two regions with differing oceanographic conditions. Journal of Sea Research 61(3):165–173.

Tilman, D., K. G. Cassman, P. A. Matson, R. Naylor, and S. Polasky. 2002. Agricultural sustainability and intensive production practices. Nature 418:671–677.

van Wenum, J. H., G. A. A. Wossink, and J. A. Renkema. 2004. Location-specific modeling for optimizing wildlife management on crop farms. Ecological Economics 48(4):395–407.

Vickery, J. A., R. B. Bradbury, I. G. Henderson, M. A. Eaton, and P. V. Grice. 2004. The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. Biological Conservation 119(1):19–39.

Wretenberg, J., A. Lindström, S. Svensson, and T. Pärt. 2007. Linking agricultural policies to population trends of Swedish farmland birds in different agricultural regions. Journal of Applied Ecology 44(5):933–941.

Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proceedings of the National Academy of Sciences USA 96:1463–1468.

Supplemental Material

Appendix

Color versions of Figs. 6–8 (*Ecological Archives* A023-008-A1).