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Abstract

Land use change is a main driver of biodiversity erosion, especially in agricultural landscapes. Incentive-based land-use policies aim at influence land-use pattern, and are usually evaluated with habitat suitability scores, without accounting explicitly for the ecology of the studied population. In this paper, we propose a methodology to define and evaluate agricultural land-use policies with respect to their ecological outcomes directly. We use an ecological-economic model to link the regional abundance of a bird species to the economic context. Policies based on such ecological economics approaches appear to be more efficient than that based on landscape evaluation, from both economic and ecological viewpoints.

Keywords: ecological-economic model, agriculture, land-use, landscape, conservation.

1   Introduction

Land-use change has been clearly identified as a main driver of changes in the abundance and geographic distribution of organisms at scales ranging from local habitats to regions, or the entire globe (Vitousek et al., 1997). In Western Europe, agriculture is clearly the most important land use (42% of the surface area), though its importance varies among countries (12% in Sweden and Finland, 52% in France and 72% in UK according to the Eurostat references). The intensification of Western European agriculture practices after WWII has been accelerated by the adoption of the Common Agricultural Policy in 1962 and it has entailed the local, national and regional extinction of numerous species of the European flora and fauna over the last 40 years, as well as profound changes in the functioning

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of these agricultural ecosystems (Krebs et al., 1999; Donald et al., 2001; Benton et al., 2002). Contrary to a widespread perception, agricultural areas harbor an important part of European biodiversity: up to 20% of the British, French and German flora (Marshall et al., 2003) and 50% of bird species (Pain and Pienkowski, 1997). Many of those species have suffered steep population declines in recent years throughout Western Europe (Donald et al., 2001; Siriwardena et al., 1998; Robinson and Sutherland, 2002). The impact of agricultural intensification on biodiversity is no longer in doubt: the declines of many species of plants, insects, and more birds at both national and European levels has being repeatedly shown to be the consequence of agricultural intensification (e.g. Donald et al., 2001; Benton et al., 2002; Robinson and Sutherland, 2002).

The commonly used strategy to conserve biodiversity and habitats has been the creation of natural reserves in publicly-owned land (Armsworth et al., 2004). This approach is however inadequate in agroecosystems where land ownership is usually private. While an important part of the budget of the Common Agricultural Policy has been allocated to schemes which aim at mitigating the environmental effects of agricultural intensification (see the article by Otte et al., 2007, for an overview and references), their effectiveness in reducing the biodiversity loss in agro-ecosystems has been moderate at best (Kleijn et al., 2001, 2006). Many of these agri-environmental schemes have involved small spatial scale actions by private owners, on voluntary basis (Ohl et al., 2008). However, affecting positively the dynamics of biological species at larger scales requires to coordinate landowners decisions, for example with market-based incentives, to encourage them to convert land or retain it in the desired use (Lewis and Plantinga, 2007). Two issues arise in turn: how to assess the influence of a policy on the spatial land-use pattern, and how to evaluate the environmental outcomes that depend on this land-use pattern? The former issue is linked to the definition of efficient policies to influence the land-use pattern in a desired way. It may involve incomplete information problems, with an uncertainty on the resulting landscape. The usual way to tackle this issue is to consider different land use scenarii, resulting in potential landscapes, to assess the influence of given policies in terms of probabilities. The latter issue raises a particular problem when considering biological conservation: How to evaluate the resulting landscape with respect to the conservation objective? Most of the studies which investigate the impact of conservation policies do so in evaluating the resulting landscape using habitat suitability scores, without considering the biological species or biodiversity explicitly (Polasky et al., 2005; De Koning et al., 2007; MacLeod and McIvor, 2008). In other words, the landscape is an output of the models and policies are defined or evaluated with respect to a landscape objective (Havlik et al., 2005, 2006; Dymond et al., 2008). However, if the initial objective was to conserve a biological population, such approaches may have limits, because they do not evaluate policies with respect to their outcomes on the biological population that has to be conserved. Ecological-Economic

modeling is a good way to overcome these limits (Wätzold et al., 2006; Drechsler and Wätzold, 2007; Drechsler et al., 2007a). In particular, Drechsler and Wätzold (2001) and Drechsler et al. (2007b,c) evaluate the outcomes of incentive-based conservation schemes using biological benefit functions, but without representing explicitly ecological dynamics, either to be able to consider simultaneously several species (Drechsler et al., 2007b) or to focus on a very specific situation (e.g., butterflies in Drechsler et al., 2007c). Tichit et al. (2007) propose a viability analysis of grazing agricultural practices and their impacts on biodiversity, using explicit ecological dynamics, but without addressing the agricultural land use issue. While all these ecological-economic approaches highlight the need for coupling ecological and economic models to improve conservation in agricultural landscapes, none propose to evaluate the ecological outcome of incentive schemes on land use using an explicit dynamic ecological model of the species under concideration.

In this paper, we present a methodology for analyzing the links between agricultural land use and biological conservation objectives, under incentive-based land-use policies and incomplete information. We develop an ecological-economic model to represent the influence of the *economic context* (i.e., prices, costs, and subsidies levels) on private owners' land-use decisions, and their outcomes on the dynamics of a biological population at a regional level. This allows us to define incentive policies focusing on the biological objective, instead of using the landscape as an indicator of ecological health.

As, in agricultural areas, land-use decisions are of private kind, an usual assumption is to consider that these decisions aim at maximizing individual gross returns, without accounting for environmental externalities. In our model, risk-neutral farmers are assumed to maximize their expected gross returns, at field level, by choosing between two potential land uses: cropland or grassland. For a given field, the expected gross return depends on two drivers: the economic context, which is the same for all fields and will be a matter of discussion later, and the agricultural quality of the field, which is heterogeneous through space and thus between fields. The higher this quality, the higher the crop yield and the higher the likelihood of using this field as a cropland in a given economic context. In an incomplete information framework, we assume that farmers know these qualities, but that the decisionmaker does not. At the regional scale, the sum of individual land-use choices generates a landscape in which a biological population evolves. The biological population is depicted with a metapopulation model where sub-populations, which growth rates depend on the local land use, are connected by dispersal processes. Grasslands are favorable to the population dynamics, while croplands are not. The population dynamics is spatially explicit, taking into account density dependence of birth-death processes and dispersal.

The economic context appears to play a major role in the land-use pattern, and thus on the population dynamics. A given context will enforce the land use,

defining a threshold such that all fields with an expected yield greater than this threshold will be used optimally as cropland. In a given economic context, the resulting landscape will thus only depend on the soil quality spatial heterogeneity. In order to evaluate the biological outcome for a given economic context and the associated land use, we compute the regional abundance of the species at equilibrium in the resulting landscape. However, in an incomplete information framework, if the agricultural soil qualities is considered to be a missing information for the policymaker, it must be considered as an uncertain variable, and it is of interest to assess the influence of the economic context on the population in terms of probabilities. For this purpose, we generate (randomly) soil quality endowment maps, and compute numerically the agricultural land use and the regional abundance of the species in a given economic context. Monte Carlo simulations give us a probability distribution of the regional abundance. Doing a sensitivity analysis of that probabilistic regional abundance with respect to the economic context, we obtain a statistical link between the biological population and the economic context.

We use our methodology to address the conservation issue. We consider that the conservation objective is to maintain the regional abundance of the population above a given threshold, with a sufficient probability. We then consider two different policy designs to achieve this objective. Firstly, we assume that the decisionmaker uses a subsidy to grassland aiming at maintaining a given landscape, focusing on habitat stability. We use this case as a benchmark representing what is mainly done in the literature. In particular, we determine the level of subsidy required to maintain the landscape in spite of an increase of crop price. Secondly, we assume that the decisionmaker uses a subsidy to grassland which objective is to conserve the population, focusing directly on the biological outcome. In particular, we determine the level of subsidy required to maintain the population above the targeted threshold. We show that this approach using ecological-economic modeling improves the design of conservation policies in two ways. On the one hand, it makes it possible to achieve the conservation objectives at a lower cost, improving the cost-efficiency of the policy. On the other hand, it ensure the achievement of the ecological objective, avoiding to maintain a landscape which is not enough suitable for the species. We illustrate these two policy designs on a case study: the protection of a Passerine bird in a French agricultural landscape in the context of increasing wheat prices.

The remainder of the paper is organized as follows. In section 2, we describe the ecological-economic model linking the agricultural land use to the biological population. In section 3, we propose a methodology based on the computation of the expected regional abundance of the species with respect to the economic context, to address the conservation issue and examine how to maintain the biological population above a targeted threshold. In section 4, we describe how our framework can be developed further by refining each component of the model to address real

conservation issues. We then conclude in Section 5 on the relevance of ecological-economic modeling, accounting explicitly for ecological dynamics, to address biological conservation issues in agricultural landscape. An appendix presents the biological parameter values with a sensitivity analysis.

2 The ecological-economic model

We consider an integrated model of agricultural land use and biological population dynamics. The agricultural land use generates a landscape. This landscape is the habitat of a biological population which has a spatially explicit dynamics.

2.1 Agricultural land use generates a landscape

We consider two types of land use: cropland (hereafter C) and grassland (hereafter G). At a regional level, the landscape results from the agricultural production decisions for all fields. At the field level, this decision depends on exogenous soil quality that will influence land use choices in farmer's decision process by determining the expected yields.

Regional soil quality map and expected yield The modeled area is represented by a map of I identically shaped, contiguous cells (hereafter fields) arranged in a 20×20 regular lattice and whose positions are defined by their centers. Each cell $i = 1, \ldots, I$ is a field of area A_i, and each field i has some inherent fertility or quality Q_i reflecting the local variability of soil quality. For example, Q might represent the quantity of Nitrogen in the soil that can be used in a sustainable way by the crop each year. This quality is assumed to influence crop yields but not grassland production.

At the regional level, the minimum expected yield (Y_{inf}) and the maximum one (Y_{sup}) are known, which makes it possible to normalize Q in the range $[0, 1]$ and to define the relationship between soil quality and expected crop yield by the following simple linear relationship[1]

$$Y(Q) = Y_{inf} + Q(Y_{sup} - Y_{inf}). \tag{1}$$

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[1]In our approach, the soil quality is represented by a single parameter Q. The agricultural production function $Y(Q)$ depends on this unique parameter. For more detailed production functions, especially the Mitscherlich-Baule function, see Frank et al. (1990), Llewelyn and Featherstone (1997) and Kastens et al. (2003). Including such details in the analysis would not modify the approach or methodology, and even not the results from a qualitative point of view. Moreover, in practice, our methodology could be applied by directly computing the potential yield for all soil qualities, and with respect to fertilizer use and other agricultural practices, using crop growth simulation tools like the agronomics models EPIC (Williams et al, 1989), STICS (Brisson et al., 2002) or CROPSYST (Stöckle et al, 2003) among others, defining maps of expected yields instead of concidering soil quality.

We assume that each farmer knows the quality of its field, but that this information is not available to the policymaker. This latter only knows the minimum and maximum potential yields in the area. Fig. 1 represents a given spatial distribution of soil qualities at the regional level.
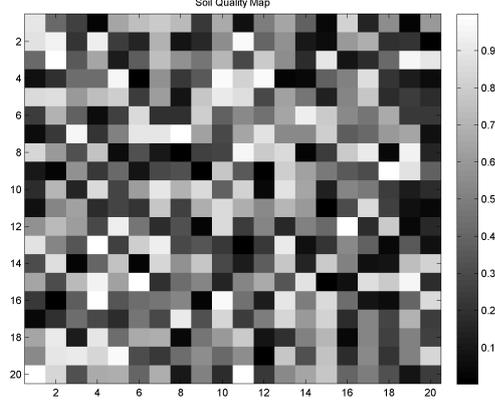

Figure 1: An example of soil quality map - The soil quality of each field i, Q_i is drawn with uniform probability distribution in $[0, 1]$.

Agroeconomic decision process Each field is assumed to be owned by a farmer that defines land-use with respect to the associated gross returns.

If a given field i is used as a cropland, i.e., land use is C, the gross return on that field is $A_i(Y(Q_i)p_C(t) - c_C(t))$, where $Y(Q_i)$ is the expected crop yield on that field in [tons/ha] given by eq. (1), $p_C(t)$ the crop selling price per unit produced ([euros/tons]), and $c_C(t)$ a cost per unit area ([euros/ha]).

If a given field i is used as a grassland, i.e., land use is G, the gross return on that field is $A_i(p_G(t) + s_G(t))$, where $p_G(t)$ is the revenue and $s_G(t)$ the subsidy per unit area of extensive grassland ([euros/ha]). We assume here that the revenue obtained from extensive grassland does not depend on the soil quality; costs are included in the revenue.

The gross return $\pi_i(t)$ of field i is thus defined as follows

$$\pi_i(t) = \begin{cases} A_i(Y(Q_i)p_C(t) - c_C(t)) & \text{if land use is} \quad C \\ A_i(p_G(t) + s_G(t)) & \text{if land use is} \quad G \end{cases} \tag{2}$$

Each farmer defines land use at field level maximizing the associated expected gross return. We assume that farmers are risk-neutral, which allows us to consider solely the expected yield, and avoid assumptions on the uncertain climatic effect that makes the yield fluctuating around its expected value.

Agricultural land use and economic context The land-use decision process thus depends on the relative gross return of both potential land uses, i.e., cropland C or grassland G. A given field i will be used as a cropland if the generated gross return is greater than that of grassland use, which reads $A_i(Y(Q_i)p_C - c_C) > A_i(p_G + s_G)$, or equivalently $Y(Q_i) > (c_C + p_G + s_G)/p_C$. It means that a field i will be used as a cropland if the expected yield $Y(Q_i)$ is greater than a threshold that depends on the economic context, i.e., prices, costs, and subsidy levels. The following proxy is used to summarize the economic context (hereafter economic proxy)

$$\mathcal{E} = \frac{c_C + p_G + s_G}{p_C}. \tag{3}$$

It corresponds to the ratio of the per area unit cost of cropland use (including opportunity costs of not using the land as grassland) ([euros/ha]) over the per production unit benefit of crop production ([euros/tons]). This proxy is homogeneous to a yield ([tons/ha]). It represents the minimum crop yield for a field to be used optimally as a cropland. As we assume that farmers know the expected yields and are optimizing their gross return at field level, in a given economic context, a given soil quality map will result in a unique landscape. The economic proxy will thus determine the landscape, as any field i having an expected crop yield greater than the economic proxy, i.e., if $Y(Q_i) > \mathcal{E}$, will be used as cropland.

Land use decisions at field level generate a landscape of croplands and grasslands. The landscape is thus a spatial pattern of fields endogenous to the model. Fig. 2 represents a given landscape.
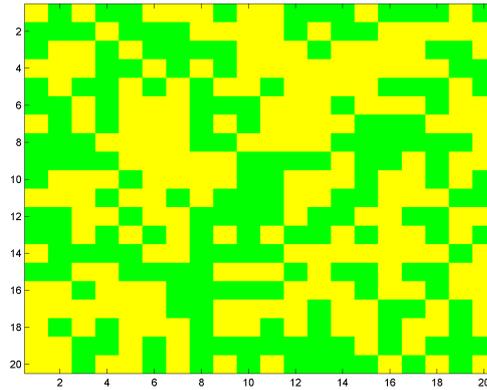

Figure 2: Landscape resulting from agricultural land use. Fields G are green (/dark) and C are yellow (/clear). That landscape has been obtained by comparing the soil quality, Q_i, to 0.5

2.2 The landscape is an habitat for a biological population

The landscape is an habitat for a biological population.[2] This population is depicted with a metapopulation model where subpopulations, whose growth is affected by the local land use type, are connected by dispersal processes.[3] At the field level, the population dynamics is positively influenced by grassland and negatively by cropland. We thus assume that the population growth is positive on grassland and negative elsewhere. Population dynamics result from a local, field-scale growth process with population regulation, and a dispersal process connecting the various sub-populations by exchanging individuals. The growth process at the field scale happens during the interval $[t, t + h)$ (with h smaller than one) and the dispersal process connecting local populations during $[t + h, t + 1)$.

Population growth The local growth in each field i, during $[t, t+h)$, is modeled according to a Ricker growth function:

$$N_{i,t+h} = N_{i,t} \exp\left(r_{i,t}(1 - \alpha_{i,t} N_{i,t}/K)\right) \tag{4}$$

where the maximum growth rate $r_{i,t}$ depends on the land use of field i at time t (with only two possible values: $r_G > 0$, or $r_C < 0$) and $\alpha_{i,t}$ is a correction term with value of zero whenever the growth rate is negative and one otherwise. Such a correction is necessary to ensure that the population always decreases when the local abundance is above the carrying capacity. That discrete-time model can generate complex dynamics (see, e.g., Kot, 2001) but only for large values of r that will not be considered here, so that it only exhibits logistic population growth. We implement a cutoff in the model: below density N_{thresh} the population size is set to zero (to avoid considering irrelevant, fractional abundances).

Dispersal The local dynamics within the I fields are linked by dispersal processes during $[t + h, t + 1)$ according to

$$N_{i,t+1} = N_{i,t+h} + \sum_{j \neq i} D_{ij}(N_{j,t+h} - N_{i,t+h}) \tag{5}$$

where D_{ij} is the proportion of individuals that disperses from field i to field j as a function of the distance between fields d_{ij} (calculated w.r.t. their centroids) and that is determined by

$$D_{ij} = \beta \frac{f(d_{ij})}{\sum_{j \neq i} f(d_{ij})} \tag{6}$$

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[2]We think mainly of small mammals or birds living in fields, but it might be also insects, or even plants.

[3]Such dispersal models are usual, for example in spatial fishery modeling (Sanchirico and Wilen, 1999, 2005).

The parameter β is the percentage of disperser individuals in a field and f is a 2D Gaussian dispersal kernel (integrating to 1) reflecting the declining strength of dispersal with distance

$$f(d) = \frac{1}{2\pi\sigma^2} \exp\left(-\frac{d^2}{2\sigma^2}\right) \tag{7}$$

The parameter σ is the dispersal range, which is expressed in units of inter-field distance (1 inter-field distance $= \frac{1}{p}$ where p is the length of the lattice, equal to 20 here). To avoid edges effects, margins are wrapped around so that dispersal happens between fields located at opposite edges of the lattice.[4]

When growth rates are unequal but constant over time, this model has a inhomogeneous positive equilibrium (see appendix) whose spatial arrangement is determined by the distances between patches and the shape of the dispersal kernel. When habitat types, and thus growth rates, are constant over time, the population as a whole is a generalized source-sink system where biomass flows from fields with positive growth rates toward fields with negative growth rates.

Fig. 3 represents the evolution of the population through time in a given fixed landscape. The population reaches an equilibrium quite quickly (before $t = 40$).
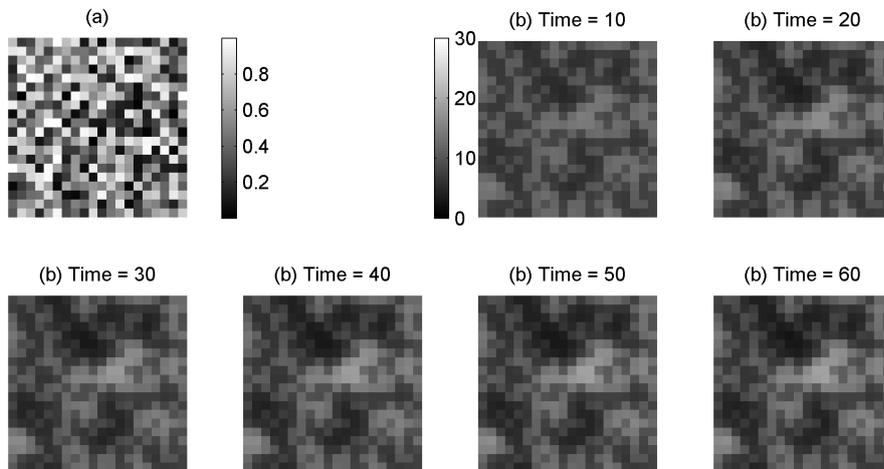

Figure 3: (a) Soil Quality Map (b) Population dynamics snapshots for various times and a landscape half-made of grassland. Parameters : $r_C = -0.1, r_G = +0.1, \beta = 0.25, \sigma = 1, K = 30, N_{thresh} = 2$

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[4]Egdes effects might be important for the population dynamics of several species in fragmented habitats. However in our case we consider that the habitat above the edges is similar, and therefore using toroidal boundaries makes sense.

Regional abundance as a function of the economic context In order to link the agricultural land use to the biological population, we aim at defining what would be the regional abundance in the long run with respect to the economic context.

In any given landscape, running the population dynamic model makes it possible to define the "virtual" long-run regional abundance on this landscape, which is the theoretical abundance toward which the population would converge if this particular landscape was maintained. The previous Fig. 3 illustrates such a long-run dynamics. The long run regional abundance is obtained by summing the fields abundances $(N_{i,t})$ at equilibrium. It reads:

$$\lim_{t \to \infty} N_t = \sum_{i=1}^{I} \lim_{t \to \infty} N_{i,t}. \tag{8}$$

This equilibrium regional abundance is taken as an indicator to assess the health of the biological population. In our simulations, the population starts at $1/3$ of the local carrying capacity K. Although we compute the equilibrium regional abundance at $t = 100$, the equilibrium is usually reached before $t = 40$ for the parameters we used (see Fig. 3). Such fast convergence justifies the use of an equilibrium abundance as a proxy of the population.

As it influences the population dynamics, the landscape will have an impact on the regional abundance. Moreover, for a given soil quality map, the landscape will vary with respect to the economic context, so will the regional abundance. Fig. 4 represents, for a given soil heterogeneity map, the long run abundance of the population in various economic context. The population dynamics seems very sensitive to the economic context. It would be of interest to define the regional abundance indicator with respect to it, i.e., with respect to the economic proxy $\mathcal{E}$.

3 Biological conservation

In this section, we examine how our ecological-economic methodology can be used to address the conservation issue. Firstly, we define a way to evaluate the probabilistic regional abundance with respect to the economic context, and introduce a conservation objective. Secondly, two kind of policy measures for biological conservation are examined. The first one aims at maintaining landscapes for habitat conservation, as usually in the literature, which can be used as a benchmark. The second one aims at protecting directly the population, using our ecological-economic results. Thirdly, a case-study is presented, for illustrating purposes.
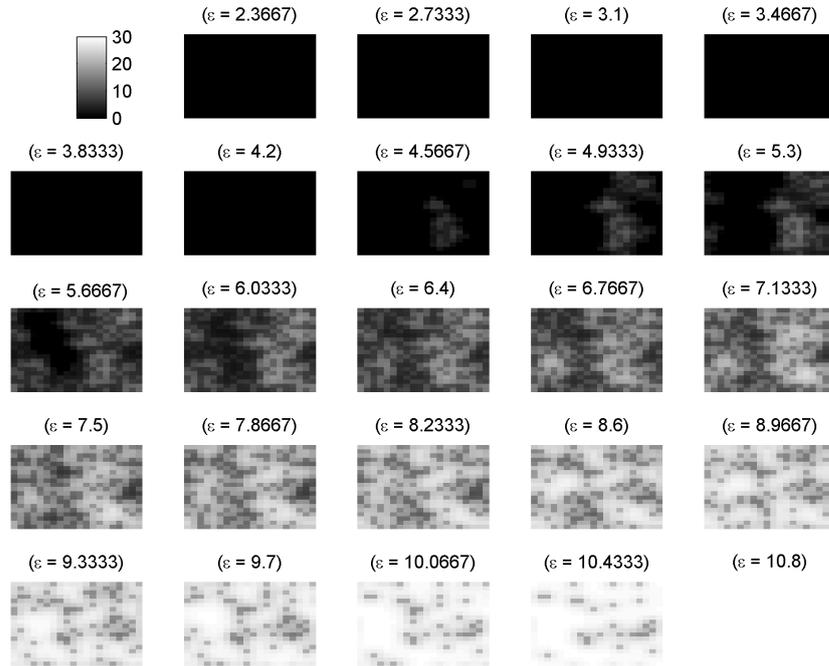
Figure 4: Spatial population patterns at equilibrium, for a given soil quality map, with respect to various economic proxies. $r_C = -0.1, r_G = +0.1, \beta = 0.25, \sigma = 1, K = 30, N_{thresh} = 2$

3.1 Conservation under incomplete information

The landscape is the result of an interaction between the economic context and a soil quality map. Under incomplete information, decisionmakers do not know the spatial distribution of soil quality. It is thus impossible for them to assess what exactly would be the landscape in a given economic context, and thus to evaluate the regional abundance of the population to be conserved. We thus assume that the soil quality map is an unknown information for them, and that they treat it as an uncertainty. This assumption has two motivations. First, it allows us to tackle the incomplete information issue. Second, it allows us to avoid the dependency of the results to a particular soil quality distribution. Under this assumption, the the link between the economic context and the regional abundance presented in the last section must be extended to a stochastic framework.[5]

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[5]This assumption could be relaxed: It would be possible to apply our methodology to a given real agricultural territory, with know soils qualities, for example using a GIS system instead of our simple grid. However, other sources of uncertainty would have to be accounted for in turn, for example to represent the uncertainty in the land-use decision process which may be more

Probabilistic regional abundance as a function of the economic context
To establish a probabilistic link between the economic context and the regional abundance, we generate randomly a large number of soil qualities maps.[6] In a given economic context $\mathcal{E}$, we compute the regional abundance, defined by eq. (8), for all the landscapes resulting from the generated soil quality maps. We then compute the frequency of a having the regional abundance at equilibrium within intervals $[n, n+\Delta n]$. Using a Monte Carlo approach, we approximate the probability distribution of abundances by the computed frequency, providing an estimator of $P(n < N(\mathcal{E}) < n + \Delta n)$. Although the population model is deterministic, the regional abundance $N(\mathcal{E})$ is, from the incompletely informed decisionmaker's point of view, a random variable depending on the random distribution of soil qualities. Fig. 5 represents some frequency distributions for various economic contexts.
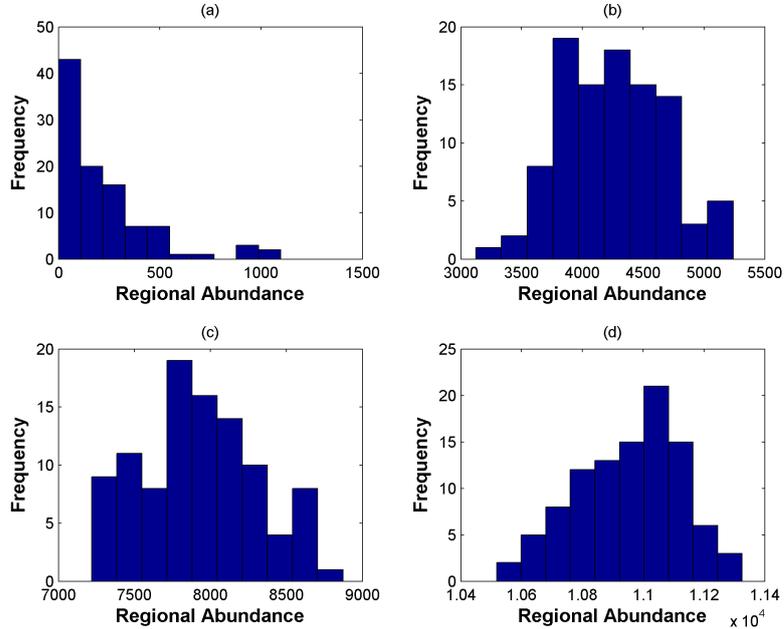

Figure 5: Frequency distribution of regional abundance for economic contexts: (a) $\mathcal{E} = 4.57$, (b) $\mathcal{E} = 6.40$, (c) $\mathcal{E} = 8.23$, (d) $\mathcal{E} = 10.07$.

A sensitivity analysis is then carried out, considering a range $[\mathcal{E}_{inf}, \mathcal{E}_{sup}]$ of economic proxies. It defines the regional abundance $N(\mathcal{E})$, defined as a statistical

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complex than suggested by the simple rule defined by eq.(2).

[6]Since we assumed the quality to be a bounded variable in $[0, 1]$, we choose the simplest quality distribution: for each field, agricultural quality is sampled from a uniform distribution on $[0, 1]$. For the sake of simplicity, we do not consider spatial autocorrelation of quality between fields, but it could easily be included. However, such an extension is not of the essence. It is of the essence to emphasize the relevance of ecological-economic modeling to address biological conservation issue, as a complement to usual approaches focusing on landscape suitability.

distribution, as a random variable depending on $\mathcal{E}$. To sum up the influence of the economic context on the regional abundance, we characterize each distribution of aundance with its mean and variance. Fig. 6 represents mean value ($\pm$ standard deviation) of the regional abundance with respect to the economic proxy.
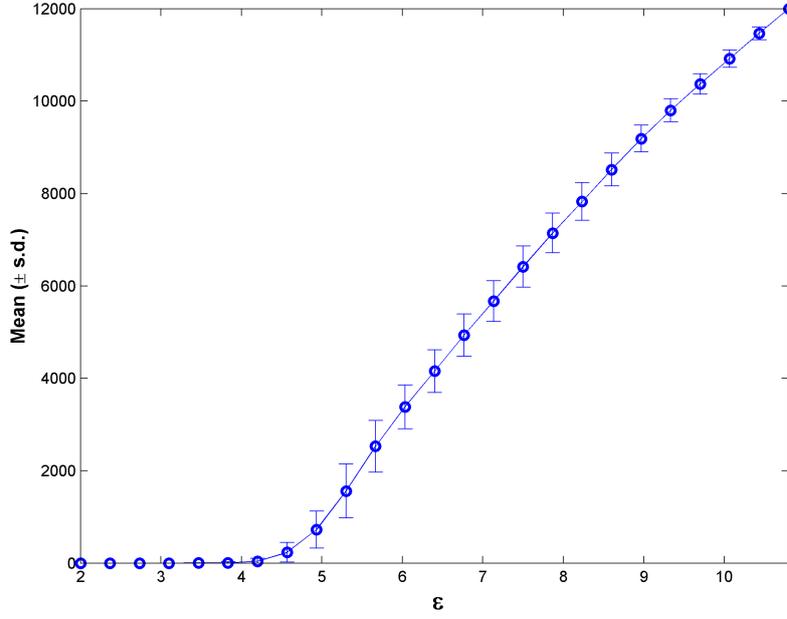

Figure 6: Expected ($\pm$ standard deviation) regional abundance N w.r.t. the economic proxy $\mathcal{E}$

The conservation objective   We assume that the conservation objective is to maintain the regional population above a threshold N_{min}, which is a target for a sustainable, healthy population. We thus want the constraint $\lim_{t \to \infty} N_t \geq N_{min}$ to be satisfied at equilibrium. As, from the decisionmaker point of view, the regional abundance is a random variable, we focus on the probability that this abundance is above the targeted threshold, i.e., $\mathbb{P}(\lim_{t \to \infty} N_t \geq N_{min})$. The probability that this objective is achieved with respect to the economic proxy $\mathcal{E}$ is represented in Fig. 7.

We also assume a given acceptable risk level (a probability of failure α). The conservation objective is thus to have $\mathbb{P}(\lim_{t \to \infty} N_t \geq N_{min}) \geq 1 - \alpha$. In our simulations we set N_{min} to $1/10$ of the maximum regional carrying capacity (i.e., the carrying capacity if all fields were used as grasslands, which is equal to $400 \times K = 12000$ in our numerical example) which implies $N_{min} = 1200$, and α to 5%.
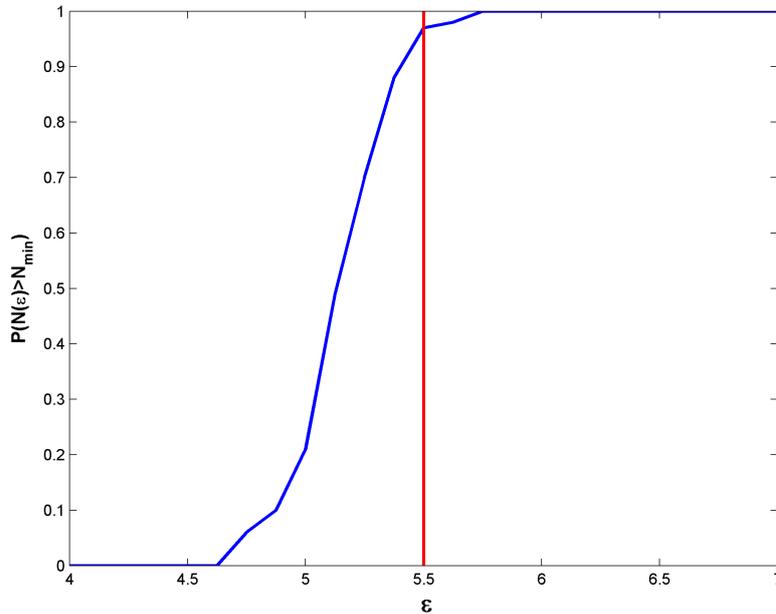
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Figure 7: Probability to achieve the conservation objective with respect to the economic context: $\mathbb{P}(\lim_{t\to\infty} N_t(\mathcal{E}) \geq N_{min})$

3.2 Mitigating agricultural market effects by incentive-based policies

At the regional level, land use changes can occur under the influence of agricultural market prices evolution. In our particular case, an increase of crop price p_C would make it profitable to use more land as cropland, as the economic proxy defining the threshold between land uses would increase. In this subsection, we examine two potential ways to cope with the consequences of such a change on the abundance of a species, by defining incentive policies to protect the biological population. A widely used instrument is the per hectare subsidy, in spite of its high cost to get efficiency (Gottschalk et al., 2007). First, we consider a case in which the decision maker focuses only on the landscape stability, with respect to some underlying habitat suitability index. Second, we consider the case in which the decision maker has information on the population dynamics, and targets the population maintain without focusing on landscape.

3.2.1 The cost of landscape stability

We first consider the case in which a decisionmaker addresses the conservation issue by providing an incentive to preserve, by maintaining grassland, a particular landscape in which the population is assumed to be safe. The crop price is assumed

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to change from p_C^1 to p_C^2, which results in a variation $\Delta p_C = p_C^2 - p_C^1$. We assume that the decisionmaker aims at maintaining the initial landscape, which resulted from the economic context associated to crop price p_C^1 and grassland subsidy s_G^1 (grassland revenue p_G and crop costs c_C are supposed to stay constant), thus the benchmark economic proxy $\mathcal{E}^\sharp = \frac{p_G + c_C + s_G^1}{p_C^1}$. Let us recall that the economic proxy is determined by economic variables (prices, costs, and subsidies), so that an increase in crop prices (the same argument could be developed for a decrease in related production costs) would imply a change in land use and then a modification of the landscape. However, such a change can be compensated for by an increase of the public subsidies to grassland. We aim at defining what should be the change of the subsidy amount $\Delta s_G = s_G^2 - s_G^1$ that would be necessary to keep the economic proxy constant in spite of the price change Δp_C, and thus keep the landscape stable.

The new economic context reads $\mathcal{E}^2 = \frac{p_G + c_C + s_G^2}{p_C^2} = \frac{p_G + c_C + \Delta s_G + s_G^1}{\Delta p_C + p_C^1}$. If the economic proxy is to be kept constant, we must have $\mathcal{E}^2 = \mathcal{E}^\sharp$, which implies

$$
\begin{aligned}
& \mathcal{E}^2 = \mathcal{E}^\sharp \\
\Leftrightarrow\quad & \frac{p_G + c_C + \Delta s_G + s_G^1}{\Delta p_C + p_C^1} = \frac{p_G + c_C + s_G^1}{p_C^1} \\
\Leftrightarrow\quad & p_C^1(p_G + c_C + \Delta s_G + s_G^1) = (p_G + c_C + s_G^1)(\Delta p_C + p_C^1) \\
\Leftrightarrow\quad & p_C^1 \Delta s_G = \Delta p_C(p_G + c_C + s_G^1) \\
\Leftrightarrow\quad & \Delta s_G = \Delta p_C \frac{p_G + c_C + s_G^1}{p_C^1} \\
\Leftrightarrow\quad & \Delta s_G = \Delta p_C \mathcal{E}^\sharp
\end{aligned}
\tag{9}
$$

It would thus be necessary to increase the subsidy level of an amount that is equal to the increase in crop prices Δp multiplied by the reference economic proxy $\mathcal{E}$ (which is the yield of the marginal land used as cropland). That simple equation gives the decisionmaker a way to compensate for an increase in crop prices so that, from the farmers' point of view, the economic proxy stays constant and therefore land use does not change, which leads to a stable landscape. In particular, if there was no initial subsidy for grassland, the subsidy to be created to maintain a landscape associated with an economic context $\mathcal{E}^\sharp$ when there is a price variation Δp_C is $s_G^{LS} = \Delta p_C \mathcal{E}^\sharp$ ("LS" for Landscape Stability).

3.2.2 The cost of population conservation

We now consider the case in which the decisionmaker aims at conserving the population, and has information on its biological dynamics and the link between the economic context and the regional abundance. Our methodology makes it possible to define and compute numerically the minimal economic proxy $\mathcal{E}^\star$ necessary to maintain the abundance above the level N_{min} with risk α, i.e., the minimal proxy

that makes it possible to achieve the conservation objective $N \geq N_{min}$ with a probability greater than $1 - \alpha$. This level is represented by the vertical line on Fig.7. It is of interest to use that information in designing conservation policies. For that purpose, for given prices and costs, we compute the level of subsidies $s_G^\star$ that would result in an economic proxy equals to $\mathcal{E}^\star$. Given $\mathcal{E}^\star$, we have

$$\mathcal{E}^\star = \frac{p_G + c_C + s_G^\star}{p_C}, \tag{10}$$

which leads to

$$s_G^\star = p_C \mathcal{E}^\star - (p_G + c_C). \tag{11}$$

Note that this subsidy level could be negative, depending on the economic context and on the biological dynamics of the species (that will influence the level of $\mathcal{E}^\star$), which means that a subsidy is not always necessary to achieve the conservation objective. In particular, it may not be necessary to compensate for a change in crop price by an increase of subsidy as long as the economic proxy stays above the threshold $\mathcal{E}^\star$.

This result allows us to compare the optimal subsidy level required to achieve the biological conservation objective to the optimal subsidy level to keep the landscape stable, i.e., s_G^{LS} defined in the previous subsection. Let us assume that we start from a situation without subsidies ($s_G^1 = 0$), characterized by an economic proxy $\mathcal{E}^\sharp = \frac{p_G + c_C}{p_C^1}$, and consider a change in crop price, from p_C^1 to p_C^2. As shown before, landscape stability requires a subsidy $s_G^{LS} = (p_C^2 - p_C^1)\mathcal{E}^\sharp = p_C^2 \mathcal{E}^\sharp - (p_G + c_C)$. From our ecological-economic results, we know that $s_G^\star = p_C^2 \mathcal{E}^\star - (p_G + c_C)$. The close mathematical form of these two expressions makes it easy to compare them. There are two possibilities:

If $\mathcal{E}^\sharp \geq \mathcal{E}^\star$, which should be the case if the initial landscape associated to the proxy $\mathcal{E}^\sharp$ was assumed to make the conservation of the population possible, the subsidy for landscape stability s_G^{LS} would be higher than $s_G^\star$. It means that the objective could be achieved with a lower subsidy level.

On the contrary, if $\mathcal{E}^\sharp \leq \mathcal{E}^\star$, the subsidy for landscape stability s_G^{LS} would be lower than $s_G^\star$, which is the minimal one required to achieve the conservation objective. It means that the conservation objective would not be achieved by a landscape stability approach.

Considering the population dynamics instead of habitat suitability can thus result in the definition of more efficient policy instruments, in the sense that the conservation objective would be achieved, with minimal cost.

3.3 An application case: High crop prices, grassland preservation, and biological conservation

In recent years, crop prices have increased, because of various factors. The main driving factor was the combination of an increasing demand on food markets, and

a reduction of stocks worldwide (due to several low production years). In order to apply our methodology with some realistic parameters, we can apply it to a simplified representation of a European agricultural landscape. We want to assess the potential impact of a change in the agricultural prices, from low commodities prices to high prices, on the long run dynamics and abundance of some Passerine bird. Our stylized model does not aim at reproducing any particular system but rather at providing some qualitative results with biologically and economically meaningful orders of magnitude. Therefore, we take the wheat production as the reference for the cereal production system, and assess the theoretical effect of a change of price on a (theoretical) small bird population. We thus consider two potential land-uses: grasslands or cropland.

This illustration is inspired from the Plaine de Niort (Deux-sèvres, France) case-study. For agronomic and economic data, we refer to Girard (2006) and Desbois and Legris (2007). For biological parameters, we refer to the appendix. The minimum expected potential yield of wheat in the area is $Y_{inf} = 2$ t/ha (tons per hectare) and the maximum potential yield is $Y_{max} = 10.8$ t/ha. We consider two different economic contexts to illustrate our approach, starting from low cereal prices to high cereal prices. In the initial context (2006 data), the price is $p_C^1 = 115$ euros/t (euros per ton). In a new context (2008 data), the price is $p_C^2 = 220$ euros/t (more favorable to wheat production). The costs of production are $c_c = 422$ euros/ha. We assume that the benefits for the grassland do not change between the two periods, and consider that it is equal to the opportunity cost of alfalfa. It leads to $p_G = 191$euros/ha (including costs). The initial subsidy level is $s_G^1 = 278$euros/ha.

With the considered biological parameters, we have $\mathcal{E}^\star = 5.667$. According to our ecological-economic model, for an economic proxy such as that of 2006 ($\mathcal{E}^1 = 7.74$) the long-run mean regional abundance of the species would be slightly above the minimal target conserving at least 1200 with 95% probability. In contrast, for the 2008 economic proxy ($\mathcal{E}^2 = 4.05$), the long-run mean regional abundance of the species would be below the targeted threshold. The change in the economic context would thus have a negative impact on the biological population, jeopardizing the conservation objective. It could motivate a public policy to ensure conservation.

If the objective of the decision maker is to maintain the 2006 landscape, according to our results, the increase of the subsidy amount should be $\Delta s_G = \Delta p_C \mathcal{E}^1 = 812.7$ euros/ha, leading to a total subsidy level of $s_G^{SL} = 1090.7$ euros/ha.[7]

If the objective of the decision maker is to conserve the population, the increase of the subsidy amount should be $s_G^\star = 633.74$, which represents "only" an increase of 355.74 euros per hectare instead of the previous 812.7 euros per hectare.

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[7]Such a level of subsidy could seem huge to the reader. However current subsidies can reach more than 500 euros per hectare of grassland in the considered area.

4 Discussion

The purpose of the developed model is not to describe any real agro-economic system and biological population, but to argue that considering explicitly the ecological dynamics, in addition to usual habitat suitability considerations, brings useful information to define conservation policies in more efficient way. We tried here to keep the model as simple as possible to illustrate our approach and how the various model components are interrelated. Specific questions need realistic models. As many practitioners are certainly more interested in constructing these specific models to conserve species rather than building a general theory of conservation in agricultural ecosystems, we suggest below a number of ways in which the model we developed could be modified to be efficiently used in practical conservation studies.

The biological component of the model assumes, for the sake of simplicity, deterministic logistic growth given a stochastic landscape spatial pattern. It has been shown, however, that even when population growth is mainly deterministically driven, the dynamics is often only qualitatively logistic so that other models (θ-logistic, stage-structured, or with delays) might be more appropriated (see, e.g., Turchin, 2003). In addition, both demographic and environmental stochasticity might drive the variation in population sizes over time. Demographic stochasticity is especially important when the population size in the smallest spatial unit considered (here the field) is small (e.g., below 40). Adding demographic stochasticity to the randomness of soil qualities would have rendered our model highly stochastic though, and we preferred to implement a cutoff at low population densities. On the other hand, environmental stochasticity is important when unpredictable environmental drivers (e.g., climate) influence population growth rates. Depending on the species and environment studied, it might be better to incorporate either demographic or environmental stochasticity, or even both (see Brännström and Sumpter (2006) for some suggestions on how to implement stochasticity).

The landscape component of the model is greatly simplified, but some of these simplifications are very easy to reverse. For instance, the regular 20 x 20 lattice is straightforwardly transformed into any irregular lattice of fields because the model is only dependent on distances between field centers. And instead of considering two crop types, one can easily extended the model to three or four crop types, or even define agricultural crop rotations instead of crop types (such as wheat/rapeseed/wheat/sunflower), which is much more realistic but dependent on the particular region considered. These modifications toward more realistic crop rotations and field geometry are quite straightforward, provided the information is available (i.e., one possesses a spatio-temporal map of crop types). In some cases, the geometry of ownership might also be important (e.g., when farmers have all their land in many little clumps instead of in one big clump). Pieces of land close to the farm or very far away might not be treated in the same way in land-use decision making (e.g., farmers might like to have their cattle close to the farm).

In such a case, the profit should be written at the farm level, not at the field spatial scale. Finally yet importantly, an agricultural landscape is not only made of fields, and many additional landscape elements, such as field margins, harbor a significant part of biodiversity. The nature and percentage of these elements in the composition of the landscape being region-specific, their modeling has to be tuned to the particular system modeled. We think, however, that only considering crop rotations and an irregular lattice, which makes only small modifications to our baseline model, might attain a reasonable amount of realism in many cases.

The modeling of agricultural production and decision-making processes might also be improved. Farmers typically use inputs (fertilizers, pesticides) to improve their yields, and the relationship between the costs and benefits of these inputs determines the level that is used, and therefore the yield - which is not a linear function of soil quality anymore. We avoid considering inputs subtleties in our model to keep the argument as simple as possible. It might be important, but only when differences in soil qualities can be countered by the use of inputs. The cost of inputs, in these cases, is surely a main driver of the intensive cropping profit. Moreover, in addition to use inputs, when farmers maximize their expected profits they might do so under a number of constraints (e.g., previous investments, labor time, risk aversion...) that could be taken into account.

Although the model we presented is highly simplified, we are confident the approach we developed is quite general, so that it can be adapted in numerous ways to cope with specific issues and to relate the regional abundance of a species to the economic context. An example of such "strategic" modelling is provided by Drechsler et al. (2007c) who investigated how cost-effective compensation payments might be designed to conserve butterflies dwelling in grasslands subjected to different moving regimes throughout the year. Our model, in contrast, is more adapted to small birds and/or mammals living in landscapes with inter-annual rather than intra-annual changes (where the land-use decision is, e.g., 'Will the farmer choose to produce wheat or alfalfa ?').

Computation of economic incentives for multi-species conservation in spatially heterogeneous habitats is presented by Drechsler et al. (2007b) using surrogates for mean individual fitnesses in various habitats to assess biological benefits. The first main difference of this approach with ours is that it neglect intraspecific competition, modelled in our framework through field-scale logistic growth (i.e., assuming individual fitnesses are linearly decreasing with local population size). The second main difference is their focus on multiple species simultaneously, which might be more desirable than single-species modelling from the policy maker point of view. The differences between the two approaches illustrates the trade-off between the number of species considered and the possible realism of the ecological model. However, we think that when the species number stays small (e.g., lower than 4) it may be possible to devise ecological-economic multispecies models for protecting

interacting species within a community (i.e. with explicit ecological interactions changing individual fitnesses and explicit dispersal). A very interesting extension of the present approach would be modelling a predator-prey community in an agricultural landscape, where the conservation target is a (patrimonial) predator dependent on its food resource to reproduce. The prey (e.g. small mammals such as voles) would be submitted to spatial variation in productivity generated by a spatial pattern of land-use as in the present work, and the predator (e.g. raptors such as buzzards, harriers) would in turn be influenced throughout prey variation generated by the land-use spatial pattern. However, the predator response to public policies might differ from that of the prey when considered alone, because of the ecological feedbacks generated by prey consumption (e.g. through the modification of population cycles).

5 Conclusion

Land-use change in agricultural landscapes is a major driver of the erosion of biodiversity. Usual conservation programs rely on incentive-based policies, such as subsidies, to influence agricultural land use. In the literature on land-use and biodiversity issue, the environmental outcomes of these programs are evaluated with habitat suitability scoring, without accounting explicitly for the ecological dynamics of studied species. In this paper, we propose a methodology for analyzing the links between agricultural land use and biological conservation objectives, under incentive-based land-use policies and incomplete information. We developed an ecological-economic dynamic model to represent the influence of the *economic context* (i.e., prices, costs, and subsidies levels) on private owners land-use decisions, and their outcomes on the dynamics of a biological population at a regional level. This allows us to define incentive policies focusing on the biological objective, instead of using the landscape as an indicator of ecological health.

We introduced an economic proxy, depending on prices, costs, and subsidies of potential land uses, to represent the economic context. We then have been able to relate a long-term frequency distribution of population regional abundances to this economic proxy, and we derived the minimal economic proxy maintaining the biological population above a target level for a given risk.

To emphasize the relevance of our approach, we described two ways to define incentives for maintaining an ecological stability when the economic context changes (Armsworth and Roughgarden, 2003). First, we evaluated the economic cost of landscape stability. Second, we evaluated the economic cost of conserving the population by focusing directly on the outcomes in terms of the conservation objective. This second cost, which is computed using our methodology, may be lower or greater then the first one. In the former case, it means that the biological objective could be achieved at a lower cost, i.e., with a higher economic efficiency. In the latter case, it means that a policy based on landscape stability would not

make it possible to achieve the conservation objective, and that focusing on the ecological outcomes results in a higher conservation efficiency. Our ecological-economic methodology thus provides a more efficient way to define conservation policies, from both economic and ecological viewpoints.

Last, we would like to argue that developing ecological-economic models of land-use and population dynamics would make it possible to study the impact of land-use changes on populations when habitat characteristic are almost constant over time (inducing constant habitat suitability index) but with strong reallocation of land uses between areas.

A   Appendix: Parameter values of the ecological model

Parameter values   We tuned the model to the dynamics of small birds living in agricultural fields. Of course, no actual species or environment might be adequately described by such a crude model (the model aims at generality) but we tried to have at least meaningful parameter values matching the orders of magnitude involved in real-world population dynamics. Parameters have thus been chosen as approximately close to those of Passerine birds (e.g., Siriwardena et al., 1998; Arlt et al., 2008). The local carrying capacity K is set to 30, the local growth rate r_G to 0.1 (+10.5 % increase in abundance) and r_C to -0.1 (-10.5 % decrease in abundance). The percentage of dispersers β is set to 0.25 and the dispersal range σ to 1 (the average dispersal range is 1 interpatch distance). A quarter of the individuals thus disperse, most of them closeby. A common drawback of real-valued difference equations, such as our population dynamics model, is that they do not allow for extinction (the abundance can be arbitrarily close to zero but still positive, taking irrelevant fractional values). Consequently we considered that there is a threshold value $N_{thresh} = 2$ below which the field abundance is set to zero, meaning that below such an abundance, the local population should go extinct. N_0 the abundance at the start for the simulation in each patch was set to $K/3$.

Sensitivity analysis   The values cited above are used as reference values, and for each reference parameter value we computed the changes in regional abundance generated by an upper or lower value. To perform this sensitivity analysis independently of the economic model, we constructed a variable Q_{thresh} which is the value of agricultural quality above which the field type is set to C (i.e. $Q_{thresh} = \frac{\mathcal{E} - Y_{inf}}{Y_{sup} - Y_{inf}}$). The parameter values tested are presented in the table below.

Parameter	Lower Value	Reference value	Upper Value
r_G	0.05	0.1	0.2
r_C	-0.2	-0.1	-0.05
K	20	30	40
N_{inf}	1	2	3
σ	0.1	1	5
β	0.1	0.25	0.5
Q_{thresh}	0.25	0.5	0.75
N_0	$K/4$	$K/3$	$K/2$

Changes generated by variations in these parameters are then summarized as mean regional abundance $\pm$ s.d. over 100 samples of soil quality maps. Let us recall that the regional carrying capacity when all patches are of type G is equal

to $400 \times 30 = 12,000$ and thus a landscape half-made of grassland would lead to a carrying capacity of $6,000$ (without dispersal). The regional abundance for the reference set of parameters is $4,345(\pm 475)$ (with dispersal), which shows the influence of dispersal processes. The table below shows the regional abundance values corresponding to upper/lower values of the parameters with respect to the reference values

Parameter	Lower	Upper
r_G	722 ± 475	$6,876 \pm 361$
r_C	$1,851 \pm 619$	$6,615 \pm 420$
K	$2,811 \pm 388$	$5,723 \pm 640$
N_{inf}	$4,292 \pm 479$	$2,262 \pm 1,217$
σ	$4,385 \pm 477$	$4,097 \pm 518$
β	$5,392 \pm 368$	$3,262 \pm 587$
Q_{thresh}	47 ± 82	$8,647 \pm 342$
N_0	$4,235 \pm 497$	$4,344 \pm 475$

Some remarks:
The percentage of fields of G type, jointly determined by the soil quality distribution and the economic proxy (soil quality threshold here) modulates the importance of the growth rates values. Dispersal is always detrimental, but its nature (either a few individuals disperse at a long range or many individuals disperse but short range) does not greatly affect the regional abundances, in contrast to the spatial pattern which is completely changed (see Fig. 8)
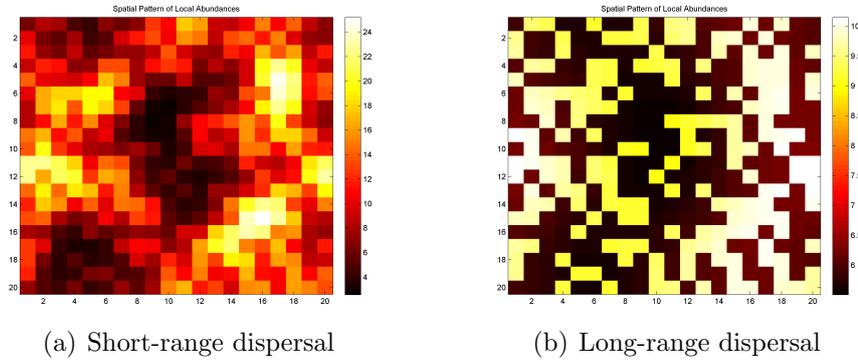

(a) Short-range dispersal

(b) Long-range dispersal

Figure 8: Effect of dispersion parameters on spatial abundance pattern

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