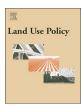
FISEVIER

Contents lists available at ScienceDirect

Land Use Policy

journal homepage: www.elsevier.com/locate/landusepol



Bioeconomic impacts of agroforestry policies in France

L. Mouysset^{a,b}, C. Rais Assa^a, J-S. Ay^c, F. Jiguet^d, R. Lorrilière^d, L. Doyen^a

- ^a CNRS, UMR 5113 GREThA, University Bordeaux IV, Avenue Léon Duguit, 33600 Pessac, France
- ^b INRA AgroParisTech, UMR 210 Economie Publique, AgroParisTech 16 rue Claude Bernard, 75005 Paris Cedex, France
- c INRA Agrosup Dijon ENESAD, UMR 1041 CESAER, Centre de recherche Dijon, Dijon, France
- ^d CNRS MNHN, UMR 7204 CESCO, 55 rue Buffon, 75005 Paris, France



ARTICLE INFO

Keywords: Biodiversity Bio-economy Land-uses Public policy Scenarios

ABSTRACT

Dealing with the erosion of terrestrial biodiversity has become of key importance in order to ensure ecosystems sustainability. Agricultural and forestry activities are one major anthropogenic driver of this decline. The underlying land-use changes result in the alteration of species habitats. In this context reconciling economic and ecological objectives of agricultural policies remains an ongoing challenge. In that respect, this paper presents the bioeconomic impacts of contrasted agricultural public policy scenarios. We developed a bio-economic model coupling an ecological model of bird dynamics with a micro-economic model of land management estimated with French data. We assessed the performances of the scenarios based on 5 ecological indicators accounting for various structural and functionnal characteristics while economic performances refer to land-use incomes. First our study confirms the potential long-term synergies between several ecological and economic objectives in grassland-based policies. Second we points out the non-trivial effect of agroforestry policies on agricultural biodiversity: despite a positive overall impact on the biodiversity population size, it implies important structural changes within the community. The choice between grassland-based policies such as in Agri-Environmental Schemes and agroforestry policies will thus depend on the ecological stakeholders' preferences.

1. Introduction

A consequence of growing anthropogenic pressure on the environment, worldwide evidence of a severe decline in biodiversity has been repeatedly reported over the last decade (Convention on Biological Diversity, 2014; Millennium Ecosystem Assessment, 2005; World Wildlife Fund, 2016). While it affects every taxa, this biodiversity loss is particularly well documented for common bird populations in Europe and is related to the intensification of farming and forestry practices (Jeliazkov et al., 2016; Chamberlain et al., 2000; Donald et al., 2001; Gregory et al., 2007; Robinson et al., 1995). One specific driver of biodiversity loss appears to be the fragmentation of habitats, defined by Fahrig (2003) as the breaking apart of natural habitats. This, along with other environmental degradation linked to human activity (for example, soil and water pollution), results in the transformation of species natural breeding and feeding sites (Benton et al., 2003; Robinson et al., 1995). These ongoing losses and transformations alter bird species nesting success and access to resources, leading to numerous extinctions (Pimm and Raven, 2000).

In this context, considering ecological consequences alongside economic objectives in public land-use policy is increasingly crucial. Over the last decades, ecological objectives have gradually been integrated in farming and forestry policy. Since 1990, the European Common Agricultural Policy (CAP) has put in place measures such as

agri-environment schemes (AES) to mitigate environmental degradation (European Commission, 2005). More recently, ecological objectives concerning forests have also been integrated in public policy, with a new European forestry strategy adopted in 2013 that aims for a common policy framework (Commission, 2013). This strategy stresses the importance of taking into account biodiversity and forest management and is today an environmental objective of the CAPs rural development policy.

However, the ecological effectiveness of these environmental measures has been widely debated. In 2006, Kleijn et al. (2006) demonstrated the mixed results of AES, which showed marginal effects on biodiversity, mainly benefitting the density of common species. The study argued that these schemes do not have a positive impact on endangered species as they only marginally protect these species habitats and resources (Kleijn et al., 2006). In 2011, another study demonstrated that AES would be more effective if they were directed towards ecosystem services (Whittingham, 2011). A further caution came in 2014, when Peer et al. (2014) raised concerns about the weaknesses of the new CAP reforms in terms of biodiversity conservation. These authors cited the decrease of the CAPs budget for rural development, coupled with the possibility of converting up to 5% of grasslands per region, as ineffective drivers for ecologically sound agriculture (Peer et al., 2014). These criticisms indicate that designing sustainable agricultural policy that reconciles production and ecological objectives remains an

ongoing challenge.

In this study, we investigated the issue of including biodiversity objectives in agricultural policy in order to promote sustainability. More specifically, we compared the bio-economic effects of an agroforestry measures to CAP grassland-based policies. To do this, we first developed a bio-economic model that combined an ecological model of bird dynamics with a micro-economic model of land management. Land-use changes over time were used as a proxy for species habitat changes, allowing the coupling of economic and ecological dynamics. Particular attention was given to the modelling of ecological dynamics in line with the results of a study by Pereira et al. (2010) that reaffirmed the need for improved biodiversity models to strengthen the role of scenarios in testing public policy. We thus designed a process-based population dynamics model that explicitly simulated species population growth by extending a model developed by Mouysset et al. (2011). We additionally modelled the dispersal of individuals in the territory based on metapopulation theory. As climate is considered to be a major driver of biodiversity variation, we extended the scope of the study by taking into account the species climate requirements (Gauzière et al., 2017; Jiguet et al., 2010; Stephens et al., 2016; Thomas et al., 2004). In a second step, we calibrated the bio-economic model with a combination of data at a national scale (mainland France): ecological data on common birds that breed in France, economic and land-use data concerning agricultural and forestry areas, and climatic data. Using this model, we assessed the economic and ecological performance of the agroecosystems over time according to different policy scenarios. This allowed us to describe potential bio-economic dynamics with quantitative economic as well as non-monetary ecological indicators at a national scale.

2. The bio-economic model

Our bio-economic model was based on the framework depicted in Fig. 1 and linked the ecological and economic dynamics through land use. A spatially explicit approach was used: the territory of France was divided into regions with different environmental metrics (i.e. land cover and climate), biological states (i.e. bird abundance) and economic characteristics (i.e. profit per hectare).

2.1. The micro-economic model

At the micro-economic scale, it was assumed that land use in region r was managed by a representative landowner. Each year, this rational regional economic agent determined the surface area $S_{r,l}$ dedicated to each land use l in order to maximize the regional profit (Eq. (1)) with a constraint of land availability (Eq. (2)) and a constraint of rigidity (Eq. (3)). The maximization program in region r was thus defined as follows:

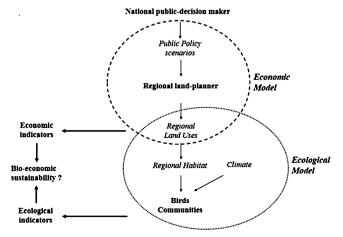


Fig. 1. The bio-economic framework.

$$\max_{S_{r,l}(t)} \Pi_r(t) = \sum_{l} S_{r,l}(t) [\pi_{r,l}(t) + \delta_l]$$
 (1)

$$\sum_{l} S_{r,l}(t) = S_r \tag{2}$$

$$|S_{r,l}(t+1) - S_{r,l}(t)| \le \xi_l S_{r,l}(t)$$
(3)

The regional profit $\Pi_r(t)$ depended on the regional area $S_{r,l}(t)$ dedicated to each land use l, the related profit per hectare $\pi_{r,l}(t)$ and the potential public incentives (i.e. tax or subsidy) δ_l . A tax was characterized by $\delta_l < 0$ and a subsidy by $\delta_l > 0$. The land availability constraint (Eq. (2)) ensured a constant regional surface area over time. The rigidity constraint (Eq. (3)) limited the amplitude of land-use change in each period and indirectly took into account both transition costs between two land-use types and technical issues.

2.2. The ecological model

To model biodiversity dynamics, we developed a spatialized metapopulation model. A metapopulation is defined as a network of interconnected sub-populations of a species (Hanski, 1998). Each region r is characterized by one sub-population. We selected two types of metapopulation dynamics to investigate: first, the reproduction of individuals within a region, and second, their dispersal between regions.

The intra-regional population dynamic (reproduction) was modelled with a Verlhust model (Verhulst, 1845) describing logistic growth (Eq. (4)):

$$N_{i,r}(t+1) = N_{i,r}(t) \left[1 + r_i - r_i \frac{N_{i,r}(t)}{K_{i,r}(t)} \right]$$
(4)

where $N_{i,r}(t)$ is the abundance of species i in region r at time t. The parameter r_i represents the intrinsic growth rate of species i and is constant for each species at a national scale. The variable $K_{i,r}(t)$ represents the carrying capacity of the region r at time t for the species i. The carrying capacity corresponds to the long-term population size of species i. We considered that the carrying capacity explicitly depends on the additive effects of land use and climate factors as follows (Eq. (5)):

$$\frac{1}{K_{i,r}(t)} = a_{i,r}^0 + \sum_{l} b_{i,l} S_{r,l}(t) + \sum_{i} c_{i,j} C_{r,j}(t)$$
(5)

where $C_{r,j}(t)$ represents the climatic variable j in region r. The parameter $a_{i,r}^0$ captures a fixed regional effect. This term implicitly describes non-included environmental effects such as proximity to the coast or elevation. The parameters $b_{i,l}$ and $c_{i,j}$ represent the response of the species i to the land use and climatic variables respectively. As environmental conditions $S_{r,l}(t)$ and $C_{r,l}(t)$ vary with time, Eq. (5) implies that the carrying capacity is dynamic.

In addition to intra-regional dynamics, we considered an inter-regional dynamic between connected regions in our spatial framework. Individuals could disperse between two regions according to a national species-specific dispersion rate defined as τ_i . We assumed the dispersal between two connected regions to be symmetric.

3. Case study and calibration

3.1. Data

We then applied this bio-economic model to R=703 small agricultural regions (SAR) in France. These were defined so that an SAR delimited a consistent area in terms of agriculture and biodiversity and was thus relatively uniform from an agro-ecological viewpoint. When the distance between two SARs was less than 30 km, we considered them to be connected, which allowed the dispersal of individuals to occur.

The SARs were defined using land-use data from the European

Environment Agencys CORINE Land Cover project, focusing on mainland France in 2000, 2006 and 2012 at the township scale (European Environment Agency, 2009). First we aggregated the 44 CORINE Land Cover types into six relevant land-use categories: urban area, annual crops, perennial crops, grasslands, deciduous (broadleaf) forests and coniferous forests. We then combined various sources to obtain economic data for each SAR. For land uses producing marketable goods (i.e. annual crops, perennial crops, deciduous forests and coniferous forests), we used annual regional data produced by the French Ministry of Agricultures Office of Statistics and Forecasting. For grasslands, we extrapolated data from the European Farm Accountancy Data Network. The rigidity parameters ξ_l (see Eq. (3)) were set with historical data. The economic data is summarized in Table 1 in App. 1. Based on the ratios between land-use changes and related profits, we fixed the parameter ξ_l in order to ensure a realistic but flexible system (see Table 2 in App. 2). Urban and perennial crop areas were assumed to be

As the biodiversity metric, we used common bird species as they (i) can be easily identified by citizens and are known to determine species richness in biodiversity indicator taxa, (ii) have a top position in the food chain and can thus signal changes occurring in the whole chain, and (iii) provide ecosystem services (Mouysset et al., 2013; Sekercioglu et al., 2008; Whelan et al., 2008). Moreover, a number of studies have shown that birds are strongly impacted by changes in farming and forestry (Chamberlain et al., 2000; Donald et al., 2001; Ormerod and Watkinson, 2000). The data on bird abundance was provided by the French National Museum of Natural History and came from the French Breeding Bird Survey (FBBS) database for the time period 2002-14. This naturalist survey is a standardized monitoring scheme in which skilled volunteer ornithologists identify and count breeding birds by song or visual contact twice a year at a given location over several years (Jiguet et al., 2012). We selected a wide pool of common species that breed in France, choosing 60 species belonging to three different groups based on their habitat preferences (Julliard et al., 2006): 14 generalist species, 23 farmland specialists and 23 woodland specialists (see Tables 3-5 in App. 3).

The climate data was obtained from the French Ministry of Environment, Energy and Sea and covered the time series from 2000 - 12. We selected two variables for climate effects: annual average temperature and annual average rainfall. The choice of time period was driven by the availability of ecological data, but it should be noted that in this short period an unusually high rate of extreme events occurred in France (summer droughts in 2003 and 2006, and winter storms in 2000, 2009 and 2010). Nevertheless, this is not necessarily problematic as it allows climatic conditions similar to longer-term projections to be observed.

3.2. Parameter estimation

We calibrated the ecological model over a timeline from $t_0 = 2002$ to T = 2012 (Eq. (6)). Bird abundance was described by the two climatic drivers and the six land-use classes (Eqs. (4) and (5)). We performed linear regression based on the least squares method in R-software (using the lm function) and estimated the model coefficients for each species i.

$$LM[N_{i,r}(t+1) \sim \tau_{i,rr}N_{i,r}(t)f_{i,r}(t) + \sum_{\bar{r} \neq r} \tau_{i,r\bar{r}}N_{i,\bar{r}}(t)f_{i,\bar{r}}(t)] \forall t \in [t_0: T]$$
(6)

where $N_{i,r}(t+1)$ is defined by Eq. (4), and $f_{i,r}(t)$ represents the dynamic described in Eqs. (4) and (5). The parameter $\tau_{i,r\bar{r}}$ represents the dispersal rate τ_i between two connected regions r and \tilde{r} . The function f is specified as follows:

$$f_{i,r}(t) = 1 + r_i - r_i \ N_{i,r}(t) \left[a_{i,r}^0 + \sum_l b_{i,l} \ S_{r,l}(t) + \sum_j c_{i,j} \ C_{r,j}(t) \right]$$
(7)

where r_i represents the growth rate of species i, and $N_{i,r}(t)$ represents the abundance of species i in region r at time t. The parameter $a_{i,r}^0$ captures a fixed regional effect. The parameters $b_{i,l}$ and $c_{i,j}$ represent the response of species i to the land use and climatic variables respectively.

The R2 coefficients of determination produced by the models for the 60 species are recorded in Tables 3, 4 and 5 in App. 3. The average R2 is 0.302 +/-0.165. To study the projected policy scenarios, we retained the 51 species showing a R2 > 0.10. Of the 60 species, 50.30% of the variable coefficients were significant, with a p-value < 0.05. Fig. 2 illustrates the temporal dynamics of historical and estimated abundance for one species from each group.

4. Scenarios and indicators

4.1. Public policy scenarios

Using the bio-economic model, we then assessed the economic and ecological performance of the 703 agroecosystems over time according to different policy scenarios. We tested these forecasted policies over a 38-year timeline from 2012-50. The five contrasting scenarios investigated were based on economic incentives.

- The Laissez-Faire scenario (*LF*) assumes no additional public policy ($\delta_l = 0 \,\,\forall \, l$). It implicitly integrates existing CAP policy in 2012 through the regional unitary profits.
- The Business As Usual scenario (*BAU*) assumes new public policy based on the model of the current CAP and the recently adopted agri-environmental measures: a subsidy for grasslands (gl) $\delta_{gl} = 200$ euros/ha, a subsidy for coniferous forests (cf) $\delta_{cf} = 200$ euros/ha, a subsidy for broadleaf forests (bl) $\delta_{bl} = 200$ euros/ha and a subsidy for annual crops (ac) $\delta_{ac} = 600$ euros/ha.
- The Intensive Farming scenario (*IF*) assumes the objectives of intensive production are reinforced, with the cultivation of annual crops supported by a higher public subsidy $\delta_{ac} = 1000 \, euros/ha$. The other incentives remain as described in the BAU scenario.
- The Green Farming scenario (*GF*) assumes efforts are made to encourage environmentally-friendly practices, by supporting the maintenance and extension of grasslands with a subsidy $\delta_{gl} = 1000$ *euros/ha*. The other public incentives remain as described in the BAU scenario.
- The Forestry Development scenario (FD) assumes the encouraged development of forests over the territory 1 . This is done by establishing a public subsidy for forest areas ($\delta_{bl}=1000$ euros/ha and $\delta_{cf}=1000$ euros/ha) and encouraging the conversion of agricultural land to forest by taxing farming activities ($\delta_{ac}=-1500$ euros/ha and $\delta_{gl}=-1500$ euros/ha).

These five land-use scenarios were run with the same climate forecast: a Status-Quo scenario in which climatic variables were kept to the 2012 values. This allowed the specific study of the impact of land-use changes in an explicit climate context, since climatic variables were taken into account in the biodiversity dynamics.

The changes in land use resulting from these different policy

 $^{^{1}\,\}mathrm{The}$ increase of forests in France in recent decades appears to be more related to agricultural abandonment than to economic opportunities from forest products. Subsidising forests is not in contradiction with past trends as these correspond to different economic mechanisms.

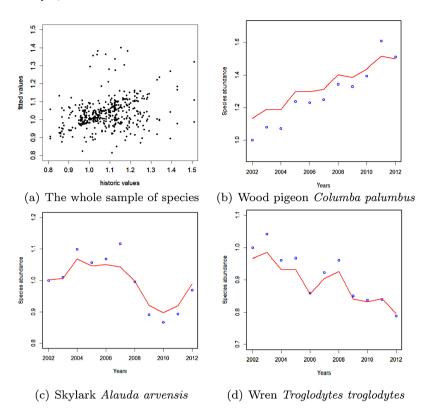


Fig. 2. Descriptive performances of the ecological model: Fig. 2(a) compares estimated values to historical ones for the 60 species considered. Example of comparison between historical (points in blue) and estimated (line in red) abundances for 3 species (Fig. 2(b): generalist, Fig. 2(c): farmland specialist and Fig. 2(d): woodland specialist). Abundances are normalized by the 2002 historical value.

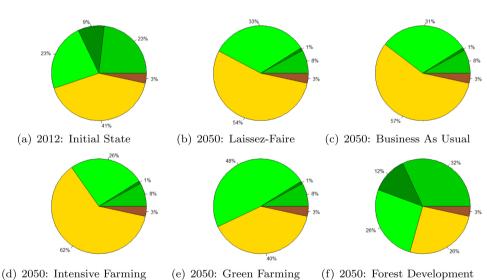


Fig. 3. National land-use patterns in the 5 scenarios. Land-use are labelled as follows: brown = Perennial Crops, yellow = Annual Crops, light green = Grasslands, green = Broadleaves Forests, dark green = Coniferous Forests.

scenarios are summarized in Fig. 3. In line with our expectations, the scenarios lead to contrasting land-use patterns in 2050. The Laissez-Faire scenario and the two intensive farming scenarios (i.e. Business As Usual and Intensive Farming) result in a large increase in areas cultivated for annual crops, in parallel with a decrease of forest and grassland areas. The extensive farming scenario (i.e. Green Farming) shows an increase of grasslands and annual crops occurring at the expense of forests. In the forest scenario (i.e. Forestry Development), woodlands develop, whereas grasslands decrease and annual crops remain stable.

4.2. Bio-economic performance

We investigated different ecological and economic indicators to assess the bio-economic performance of the five policies over time.

Economic indicators

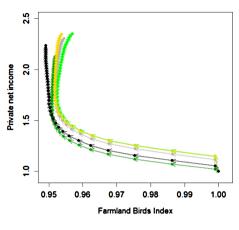
The economic situation was assessed by calculating yearly profits at a national scale as in Eq. (8).

$$\Pi_{\text{Nat}}(t) = \sum_{r} \sum_{l} S_{r,l}(t) [\pi_{r,l}(t) + \delta_{l}]$$
(8)

Biodiversity indicators

To assess ecological performance, we combined two complementary types of ecological indicator: the dynamics and the structure of the selected bird communities.

First, we computed for each of the three species groups (generalist, farmland and woodland) an official European Bird Indicator as defined by Balmford et al. (2005). Based on a geometric mean of growth rates,



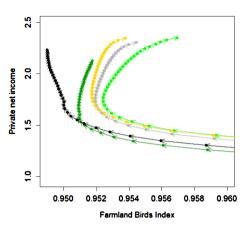


Fig. 4. Temporal bio-economic performances of the 5 public policy scenarios. Scenarios are labelled a follows: black = Laissez-Faire Scenario, grey = Business As Usual Scenario, yellow = Intensive Farming Scenario, light green = Green Farming Scenario, dark green = Forestry Development Scenario. The arrow indicates the sense of the temporal dynamic.

(a) FBI vs Profits: 2012 - 2050

(b) FBI vs Profits: 2020 - 2050

this multi-species indicator describes community dynamics. It was computed as follows for the F=17 farmland specialists (Eqs. (9) and (10)), the G=14 generalists (Eqs. (9) and (11)) and the W=21 woodland specialists (Eqs. (9) and (12)):

$$N_{i,\text{Nat}}(t) = \sum_{r} N_{i,r}(t) \tag{9}$$

where the variable $N_{i,Nat}(t)$ represents the national abundance of species i at time t.

The national Farmland Bird Indicator (FBI):

$$FBI_{Nat}(t) = \prod_{i=1}^{F} \left(\frac{N_{i,Nat}(t)}{N_{i,Nat}(t_0)} \right)^{\frac{1}{F}}$$
(10)

The national Generalist Bird Indicator (GBI):

$$GBI_{Nat}(t) = \prod_{i=1}^{G} \left(\frac{N_{i,Nat}(t)}{N_{i,Nat}(t_0)} \right)^{\frac{1}{G}}$$
(11)

The national Woodland Bird Indicator (WBI):

$$WBI_{Nat}(t) = \prod_{i=1}^{W} \left(\frac{N_{i,Nat}(t)}{N_{i,Nat}(t_0)} \right)^{\frac{1}{W}}$$
(12)

where t_0 is the year of reference (here $t_0 = 2002$).

Second, we calculated two structural indicators assessing the functional state of the community (the Community Trophic Indicator and the Community Specialization Indicator) with:

$$N_{\text{tot},r}(t) = \sum_{i} N_{i,r}(t) \tag{13}$$

where $N_{tot,r}(t)$ represents the number of individuals in region r at time t. The national Community Trophic Indicator (Eq. (15)) specified the communitys trophic level and was calculated as an average of the

communitys trophic level and was calculated as an average of the abundance of each species weighted by the species trophic index (see Tables 3, 4 and 5 in App. 3). This trophic index provided information on the position of each species in the trophic chain based on diet information as in Julliard et al. (2006).

$$CTI_r(t) = \sum_{i} \frac{N_{i,r}(t)}{N_{tot,r}(t)} STI_i$$
(14)

where the parameter STI_i represents the Species Trophic Index of the species i (Julliard et al., 2006).

$$CTI_{Nat}(t) = \frac{1}{R} \sum_{r=1}^{R} CTI_r(t)$$
(15)

The Community Specialization Indicator (Eq. (17)) assessed the communitys specialization for specific habitats. Similar to the

Community Trophic Indicator, it was calculated as an average of the abundance of each species weighted with the Species Specialization Index (SSI) (see Tables 3, 4 and 5 in App. 3). This index is based on the species habitat preferences as in Julliard et al. (2006).

$$CSI_r(t) = \sum_{i} \frac{N_{i,r}(t)}{N_{tot,r}(t)} \exp(SSI_i)$$
(16)

where the parameter $exp(SSI_i)$ represents the Species Specialisation Index of the species i (Julliard et al., 2006).

$$CSI_{Nat}(t) = \frac{1}{R} \sum_{r=1}^{R} CSI_r(t)$$
(17)

5. Results

5.1. Bio-economic performance of the policy scenarios

In our investigation of the bio-economic impacts of the five policy scenarios, we assessed both ecological and economic outcomes. From an ecological point of view, we focused on the European Farmland Bird Indicator (FBI), which has been adopted by the EU and other organizations as an indicator of the general quality of the farmed environment. As shown in Fig. 4(a), a short-term analysis (i.e. the first five simulated years, 2014-2019) does not differentiate between the scenarios on an ecological basis. In each scenario, the FBI decreases with the same amplitude in the first years of simulation. This residual decrease is not driven by policy-induced land use change but is due to the inertia of ecological dynamics.

The second period (2020-50) exhibits more contrasting patterns (Fig. 4(b)), revealing differences between farming and forestry-oriented policies. In terms of FBI performance, farming scenarios (i.e. Business As Usual, Intensive Farming and Green Farming) yielded better ecological performance, with an inversion of the downward FBI trend in the long-term. The best policy scenario for encouraging an upward trend in the FBI was extensive Green Farming. Interestingly, the Forestry Development policy obtained the worst performance, regarding both ecological and economic indicators, in comparison with Intensive Farming and Green Farming. However, it had a better FBI result than the Laissez-Faire scenario.

Fig. 5 illustrates the long-term bio-economic trade-offs of the policies. First, it highlights the general positive effect of any of the landuse policies on biodiversity, as the Laissez-Faire scenario (i.e. no public policy implemented) yielded the lowest long-term ecological performance. It also highlights potential synergy between profit and biodiversity in the long term. Indeed, the most ecologically effective scenario proves also to be the most economically effective: Green Farming ensured both the best long-term profits and the best ecological

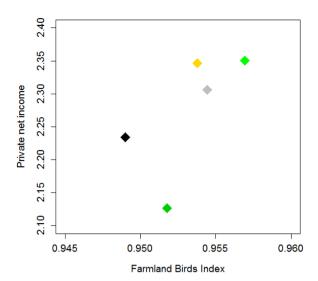


Fig. 5. Long-term bio-economic trade-off in 2050: FBI_{Nat} (2050) and Π_{Nat} (2050). Scenarios are labelled a follows: black = Laissez-Faire Scenario, grey = Business As Usual Scenario, yellow = Intensive Farming Scenario, light green = Green Farming Scenario, dark green = Forestry Development Scenario.

performance. While several scenarios had relatively similar economic results (the Business As Usual, Intensive Farming and Green Farming scenarios), they resulted in contrasting ecological performance as the land uses are different.

5.2. Contrasting bird communities

Additionally, we investigated the consequences of each scenario on bird communities, by comparing the impacts of different policies on a set of ecological indicators. The general impact of the five scenarios on the bird community is summarized in Fig. 6. This shows that a scenarios ranking in terms of ecological performance changes depending on the biodiversity indicator. No specific scenario resulted in the best performance across every indicator. The Forestry Development scenario was

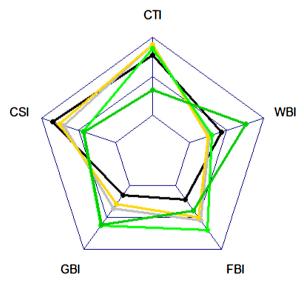


Fig. 6. Ecological performances of the 5 public policy scenarios in 2050. Biodiversity indicators are labelled as follows: CSI = Community Specialisation Indicator, CTI = Community Trophic Indicator, GBI, FBI and WBI = Generalist, Farmland and Woodland Bird Indicators. Scenarios are labelled as follows: black = Laissez-Faire, grey = Business As Usual, Light green = Green Farming, Gold = Intensive farming, Dark green = Forest development.

the only policy that increased the woodland bird indicator (WBI). It was also the only scenario that simultaneously increased the three population size indicators (FBI, GBI and WBI) compared to the Laissez-Faire scenario. However, regarding the trophic and specialization structural indicators (CTI and CSI), its performance was weak; in fact, it was the only scenario that led to a decrease in CTI. This result seems counterintuitive, as woodland species have on average a higher trophic index than the other species groups (6.085 for the woodland specialists compared to 5.788 for the farmland specialists and 5.634 for the generalists).

To explain this CTI result, we explored the relative impacts of the Forestry Development scenario on the species trophic level for the three species groups. Fig. 7 shows that farmland and woodland specialist species decrease relative to generalist species. In other words, the increase in population size of farmland and woodland specialists is smaller than the increase in population size of generalist species. This result is consistent with Fig. 6. However, we observed that the population increase in generalist species is mainly in favour of generalists with a low trophic level. This lower trophic level in the generalist group is stronger than the higher trophic level in the woodland specialist group, yielding a decrease in the Community Trophic Index. As a consequence, the Forestry Development scenario has a strong effect on the community biodiversity structure.

6. Discussion

6.1. Bio-economic model of agroecosystem dynamics

In this study, we developed a bio-economic model integrating an ecological model of bird dynamics coupled with a micro-economic model of land management. Land-use changes over time were used as a proxy for species habitat changes, allowing the exploration of economic and ecological dynamics. Particular attention was given to modelling the ecological dynamics in line with the conclusions of Pereira et al. (2010), which reaffirmed the need for more complex ecological models in public policy analysis. To do this, we developed a process-based model of population dynamics that explicitly simulates species population growth by extending a model proposed by Mouysset et al. (2011). We additionally modelled the dispersal of individuals through the territory using metapopulation theory, and, as climate is considered to be a major driver of biodiversity variation, we extended the scope of the study by taking into account the species climatic requirements (Gauzière et al., 2017; Jiguet et al., 2010; Stephens et al., 2016; Thomas et al., 2004).

The bio-economic parameters were estimated at the scale of mainland France by combining ecological data on common bird species, economic and land-use data for agricultural and forestry areas, and climate data. This study contributes to the field of bio-economic modelling of agroecosystems by virtue of the explicit integration of complex ecological dynamics (including both temporal and spatially explicit processes) with two types of explicative variables, land-use changes and climate variables. Our statistical analysis demonstrated satisfying first results regarding the significance of the parameters and the R2 of the model. However, it would be interesting to extend the study to compare different mechanistic ecological functions, especially regarding dynamics, as in Mouysset et al. (2016). The analysis of spatial dispersion could also be deepened by linking the dispersion process to the explicative variables. Currently, the dispersion rate is independent of the land use and climate contexts, but integrating these could reinforce the trends observed in the analysis.

Finally the land use is currently aggregated on a high level (6 land use classes). Refining this typology could allow to highlight more detailed and specific processes since these classes cover a certain heterogenity. Regarding grasslands, it could be interesting for example to

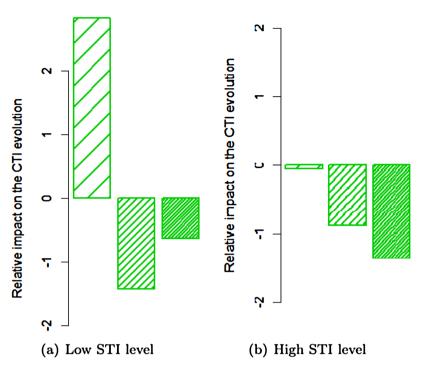


Fig. 7. Relative impact of the 3 species groups on the evolution of the Community Trophic Indicator in the FD scenario and function of the species trophic level. Species groups (from left to right): Generalist, Farmland specialist, Woodland specialist.

distinguisgh High Nature Value which are determinant for many meadow birds. Regarding forests, it would be interesting to consider the age of the forest in addition to the typ of trees. Indeed woodpeckers for example need for their nests not forests in general but forests with old trees. Finally regarding croplands, information about inputs and pesticides could constitute a relevant information to precise the effect of land use on bird communities.

6.2. Consequences of promoting forestry in agricultural policy

A key contribution of the study regards the comparison of public policy scenarios. The results add to knowledge about the long-term trade-offs between economically productive activity and biodiversity in terrestrial ecosystems. Our findings demonstrate that potential synergy is possible between profitability and terrestrial biodiversity: adequate long-term policy, while costly in the mid-term, can improve ecological performance in parallel with economic performance (Bullock et al., 2006; Mouysset et al., 2012; Steffan-Dewenter et al., 2007). The extensive Green Farming scenario showed the best performance, maximizing both the FBI and profit in the long term. This result confirms the overall beneficial impact of an increase in grasslands (Doxa et al., 2010; Mouysset, 2014). In an objective of maximizing the FBI as well as economic profit in the long term, public policy supporting extensive farming and grasslands should be favoured.

In terms of the second pillar of the CAP, which focuses on rural development (Commission, 2013), we also investigated the integration of agroforestry policies and forest biodiversity in the traditional scenarios that subsidize croplands or grasslands. Our findings show that extensive farming policy supporting grasslands is adverse for woodland specialist species. In contrast, policies favouring forestry development are positive for this species group, while also positive for farmland specialist species and generalist species. Yet while agroforestry policies offer interesting potential regarding biodiversity, the findings indicate

that they had a strong negative impact on the mean trophic index of the community, generating deep structural modifications. These non-trivial effects of agroforestry policies on agricultural biodiversity (a positive overall impact on the population size of a wide range of species, but significant structural changes within the species community) mean that the choice between grassland-based policies such as agri-environmental schemes and agroforestry policies will depend on the objectives of ecological stakeholders.

To extend our public policy analysis, it would be interesting to investigate the conclusions in a context of urbanization and of climate change. In the current scenarios, urban areas and perennial crops were kept constant. But while areas cultivated with perennial crops are indeed very rigid because of high conversion costs, this hypothesis for urban areas could be relaxed, at least on the time horizon to 2050. Currently, the development of urban areas in France is mostly at the expense of agricultural areas. As a consequence, the pressure on agricultural land use increases. In this context, we might expect incentives to be required to limit urbanization. Another major driver of biodiversity trends (Thomas et al., 2004) is climate change. In this study, we retained a Status-Quo climate scenario, but developing contrasting climate change scenarios in parallel with different public policies would provide valuable insights into the future of terrestrial biodiversity. As climate is already included in our modelling framework, we could investigate a variety of climate-related scenarios. The possibility of mitigating global warming through specifically targeted land-use policies could be examined and compared with other studies (Ay et al., 2014; Gauzière et al., 2017; Princé et al., 2013). The northward-shift hypothesis (the northward shift of a species distribution range due to climate change) could also be tested with our spatialized model (Gauzière et al., 2017; Hitch and Leberg, 2007; Perry, 2005). Equally, integrating information about forest management in addition to forest cover could improve the quality and estimating power of our model, allowing us to refine our forestry development scenarios or investigate

new agroforestry policies. Indeed, improving forest management practices (e.g. through new types of management, new species or adapted clones, etc.) could potentially increase profit from forest activities without increasing forest areas, leaving space for green farming activities, for instance.

6.3. Considering several biodiversity indicators in public policy

Comparing bio-economic contributions offers some theoretical insights that could inform the ongoing debate on how to effectively integrate biodiversity objectives in the design and evaluation of public policy. In order to understand the interactions between public policy and biodiversity, we considered five ecological indicators that represent various biodiversity components. The different policy scenarios led to contrasting results depending on the biodiversity metric investigated. In that respect, we can conclude that the specific choice of measures policymakers put in place should be guided by the biodiversity objectives they seek to support. For example, farmland species are better protected by extensive farming scenarios, whereas woodland and generalist species show better results within a forestry scenario. The community trophic level, reflecting the functional state of the community, is improved in farming scenarios. These examples underline the necessity of adapting the public policy strategy in order to maximize the results for the biodiversity component specifically targeted.

The results also highlight that relying on one specific indicator for the design and evaluation of public policy is not neutral from an ecological viewpoint. For example, our findings emphasized that the species redistribution occurring in the Forestry Development scenario was not visible solely through an FBI analysis. This result is in line with studies highlighting the limits of the FBI when taking into account different types of species or their habitat requirements (Butler et al., 2010, 2012; Monnet et al., 2014; Stjernman et al., 2013). Yet these impacts should not be neglected since they can reveal a loss of resilience in the community. This demonstrates a need for the inclusion of multiple biodiversity metrics in addition to the FBI when developing and evaluating public policy (Mouysset et al., 2012).

To conclude, our findings emphasize the need for a multi-criteria approach in order to broadly assess the performance of a public policy scenario. In addition to the economic and ecological criteria used in this study, analysing the impacts of each policy scenario in terms of the provision of ecosystem services would provide further insights into their general performance. Investigating the impacts of policy in terms of ecosystem services (such as the cultural value of birds, carbon sequestration, or water and soil quality regulation) would provide valuable arguments in discussions concerning their inclusion in the decision-making process (Bateman et al., 2013; Goldstein et al., 2012; Whittingham, 2011). The framework designed for this study allows a wide evaluation of the performance of different policy scenarios in terms of ecosystem services, which would provide interesting findings at the scale of mainland France.

Acknowledgements

This study received funding from the French LabEx COTE (Laboratory of Excellence: Evolution, adaptation and governance of continental and coastal ecosystems and from the French OASIC project SENTIER (CNRS fundings). We would also like to thank all the volunteers who participated in the French national breeding bird survey.

Appendix A. Economic data

Table 1

Table 1
Summarizing table of economic data

	Annual crops	Grasslands	Perennial crops	Coniferous forets	Broadleaves forests
Mean (euros/ha)	5992.997	4047.529	42391.734	224,190	119,764
Minimum (euros/ha)	331,293	0.164	30.670	0.315	0.105
Maximum (euros/ha)	939640.454	224804.889	6330000	4053.797	6068.733
Standard deviation	39621.656	10358.904	358544.918	243.072	483.673

Appendix B. Set of the rigidity parameters.

Table 2

Table 2 Set of ξ_l . Land-uses are labelled as follows in the entire paper: bl = Broadleaves, cf = Conifers, ac = Annual Crops, gl = Grasslands, pc = Perennial Crops, urb = Urban

ξы	ξcf	ξ_{ac}	ξ_{gl}	ξ_{pc}	ξ_{urb}
0.03	0.08	0.15	0.06	0	0

Appendix C. The species of the study and their caracteristics

Tables 3–5

Table 3Generalist species summary table

Species	STI	SSI	R2
Wood Pigeon Columba palumbus	2.746	0.300	0.508
Carrion Crow Corvus corone	4.527	0.281	0.352
Cuckoo Cuculus canorus	7.389	0.043	0.499
Chaffinch Fringilla coloebs	3.004	0.272	0.507
Jay Garulus glandarius	5.585	0.444	0.296
Melodious Warbler Hippolais polyglotta	7.029	0.700	0.288
Nightingale Luscinia megarhynchos	7.389	0.470	0.655
Golden Oriole Oriolus oriolus	7.029	0.473	0.284
Eurasian blue Tit Parus caeruleus	6.050	0.351	0.282
Great Tit Parus major	6.360	0.295	0.425
Green Woodpecker Picus viridis	7.389	0.384	0.338
Dunnock Prunella modularis	4.482	0.495	0.414
Blackcap Sylvia atricapilla	4.953	0.316	0.599
Blackbird Turdus merula	4.953	0.234	0.497

Table 4 Woodland specialist species summary table

Species	STI	SSI	R2
Wood Pigeon Columba palumbus	2.746	0.300	0.326
Short tead Treecreeper Certia brichydactyla Brehm	7.389	0.622	0.326
Eurasian treecreeper Certhia familiaris	7.029	1.889	0.036
Hawfinch Coccothraustes coccothraustes	2.858	0.984	0.205
Great spotted woodpecker Dendrocopus major	5.474	0.638	0.369
Middle spotted woodpecker Dendrocopus medius	5.474	1.921	0.242
Black woodpecker Dryocopus martius	7.389	1.235	0.093
European robin Erithacus rubecula	6.234	0.484	0.438
Coal tit Parus ater	4.953	1.386	0.378
European crested tit Parus cristatus	4.953	1.617	0.195
Marsh tit Parus palustris	5.474	0.988	0.161
Western Bonelli's warbler phylloscopus bonelli	7.389	0.859	0.487
Chiffchaff Phylloscopus collybita	7.029	0.460	0.508
Wood warbler Phylloscopus sybillatrix	7.029	1.720	0.276
Willow warbler Phylloscopus troquillus	7.029	1.118	0.458
Grey-headed woodpecker Picus canus gmelin	7.389	1.317	0.125
Bulfinch Pyrrhula pyrrhula	3.004	1.053	0.096
Goldcrest Regulus regulus	7.389	1.081	0.235
Nuthatch Sitta europaea	7.389	1.460	0.328
Sardinian warbler Sylvia melanocephala	5.474	0.756	0.493
Wren Troglodytes troglodytes	7.389	0.372	0.632
Song Trush Turdus philomelos Brehm	4.807	0.402	0.449
Mistle Trush Turdus viscivorus	4.711	0.518	0.249

Table 5Farmland specialist species summary table

Species	STI	SSI	R2
Wheatears Oenanthe oenanthe	7,030	1,704	0,035
Grey Partridge Pendix pendix	3.004	2.196	0.505
Winchat Saxicola rubetra	7.389	1.463	0.054
Stonechat Saxicola torquata	7.389	0.776	0.101
Whitethroat Sylvia communis Latham	4.953	0.654	0.343
Ноорое Ирира ерорѕ	7.389	0.607	0.185
Lapwing Vanellus vanellus	6.686	2.228	0.090
Skylark Alauda arvensis	3.490	1.155	0.570
Red-legged Partridge Alectoris Rufa	3.004	1.097	0.280
Tawny Pipit Anthus campestris	7.029	1.996	0.213
Meadow Pipit Anthus prathensis	5.755	0.375	0.017
Buzzard Buteo buteo	18.174	0.495	0.151
Linnet Canduelis cannabina	2.858	0.697	0.144
Rook Corvus frugilegus	5.104	0.846	0.209
Quail Coturnix coturnix	3.387	1.524	0.094
Cirl Bunting Emberiza cirlus	3.669	0.586	0.394
Yellow Hammer Emberiza citrinella	3.669	0.711	0.474

(continued on next page)

Table 5 (continued)

Species	STI	SSI	R2
Firecrest Regulus ignicappilus	7.389	0.681	0.145
Crested Lark Galerida cristata	4.710	1.711	0.324
Red-backed Shrike Lannius collunio	8.585	1.141	0.076
Wood lark Lullula arborea	4.482	0.903	0.296
Corn Bunting Miliaria callandra	3.597	1.464	0.374
Yellow Wagtail <i>Motacilla flavia</i>	7.3	2.091	0.249

References

- Ay, Jean-Sauveur, Chakir, Raja, Doyen, Luc, Jiguet, Frdric, Leadley, Paul, 2014. Integrated models, scenarios and dynamics of climate, land use and common birds. Clim. Change 126 (1-2), 13–30.
- Balmford, A., Bennun, L., Ten Brink, B., Cooper, D., Cote, I.M., Crane, P., Dobson, A., Dudley, N., Dutton, I., Green, R.E., et al., 2005. The convention on biological diversity s 2010 target. Science 307.
- Bateman, I.J., Harwood, A.R., Mace, G.M., Watson, R.T., Abson, D.J., Andrews, B., Binner, A., Crowe, A., Day, B.H., Dugdale, S., Fezzi, C., Foden, J., Hadley, D., Haines-Young, R., Hulme, M., Kontoleon, A., Lovett, A.A., Munday, P., Pascual, U., Paterson, J., Perino, G., Sen, A., Siriwardena, G., van Soest, D., Termansen, M., 2013. Bringing ecosystem services into economic decision-making: land use in the United Kingdom. Science 341 (6141), 45–50.
- Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol. Evol. 18 (4), 182–188.
- Bullock, James M., Pywell, Richard F., Walker, Kevin J., 2006. Long-term enhancement of agricultural production by restoration of biodiversity: Restoring biodiversity enhances production. J. Appl. Ecol. 44 (1), 6–12.
- Butler, Simon J., Freckleton, Robert P., Renwick, Anna R., Norris, Ken, 2012. An objective, niche-based approach to indicator species selection: Objective indicator species selection. Methods Ecol. Evol. 3 (2), 317–326.
- Butler, S.J., Boccaccio, L., Gregory, R.D., Vorisek, P., Norrisa, K., 2010. Quantifying the impact of land-use change to European farmland bird populations. Agric. Ecosyst. Environ. 137, 348–357.
- Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C., Shrubb, M., 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. J. Appl Ecol. 37 (5), 771–788.
- Commission, European 2013. A new EU Forest Strategy: for forests and the forest-based sector.
- Convention on Biological Diversity 2014. Global biodiversity outlook 4: a mid-term assessment of progress towards the implementation of the strategic plan for biodiversity 2011-2020.
- Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proc. Royal Soc. B: Biol. Sci. 268 (1462), 25–29
- Doxa, Aggeliki, Bas, Yves, Paracchini, Maria Luisa, Pointereau, Philippe, Terres, Jean-Michel, Jiguet, Frdric, 2010. Low-intensity agriculture increases farmland bird abundances in France: High nature value farmland birds. J. Appl. Ecol. 47 (6), 1348–1356
- European Commission 2005. Agri-environment Measures. Mar.
- European Environment Agency 2009. CORINE Land Cover France.
- Fahrig, L., 2003. Effects of Habitat Fragmentation on Biodiversity. Annu. Rev. Ecol. Evol. System. 34 (1), 487–515.
- Gauzière, P., Princé, K., Devictor, V., 2017. Where do they go?, The effects of topography and habitat diversity on reducing climatic debt in birds. Global Change Biol. 23, 2218–2229.
- Goldstein, J.H., Caldarone, G., Duarte, T.K., Ennaanay, D., Hannahs, N., Mendoza, G., Polasky, S., Wolny, S., Daily, G.C., 2012. Integrating ecosystem-service tradeoffs into land-use decisions. Proc. Natl. Acad. Sci. 109 (19), 7565–7570.
- Gregory, R.D., Vorisek, P., Van Strien, A., Gmelig Meuling, A.W., Jiguet, F., Fornasari, L., Reif, J., Chylarecki, P., Burfield, I.J., 2007. Population trends of widespread woodland birds in Europe. Ibis 149 (s2), 78–97.
- Hanski, I., 1998. Metapopulation dynamics. Nature 396 (6706), 41-49.
- Hitch, Alan T., Leberg, Paul L., 2007. Breeding distributions of North American bird species moving north as a result of climate change. Conserv. Biol. 21 (2), 534–539.
- Jeliazkov, A., Mimet, A., Chargé, R., Jiguet, F., Devictor, V., 2016. Impacts of agricultural intensi fi cation on bird communities: New insights from a multi-level and multi-facet approach of biodiversity. Agric. Ecosyst. Environ. 216, 9–22.
- Jiguet, F., Gregory, R.D., Devictor, V., Green, R.E., Vo Ek, P., Van Strien, A., Couvet, D., 2010. Population trends of European common birds are predicted by characteristics of their climatic niche. Global Change Biol. 16 (2), 497–505.
- Jiguet, F., Devictor, V., Julliard, R., Couvet, D., 2012. French citizens monitoring ordinary birds provide tools for conservation and ecological sciences. Acta Oecol. 44 (Oct), 58–66.

- Julliard, R., Clavel, J., Devictor, V., Jiguet, F., Couvet, D., 2006. Spatial segregation of specialists and generalists in bird communities. Ecol. Lett. 9 (11), 1237–1244.
- Kleijn, D., Baquero, R.A., Clough, Y., Daz, M., Esteban, J., Fernndez, F., Gabriel, D., Herzog, F., Holzschuh, A., Jhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M., Yela, J.L., 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries: Biodiversity effects of European agri-environment schemes. Ecol. Lett. 9 (3), 243–254.
- Millennium Ecosystem Assessment 2005. Ecosystems and human well-being: synthesis.

 Monnet, A.C., Jiguet, F., Meynard, C., Mouillot, D., Mouquet, N., Thuiller, W., Devictor,
 V., 2014. Asynchrony of taxonomic, functional and phylogenetic diversity in birds:
 Asynchrony of bird diversities. Global Ecol. Biogeogr. 23 (7), 780–788.
- Mouysset, L., 2014. Agricultural public policy: Green or sustainable? Ecol. Econ. 102 (June), 15–23.
- Mouysset, L., Doyen, L., Jiguet, F., Allaire, G., Leger, F., 2011. Bio economic modeling for a sustainable management of biodiversity in agricultural lands. Ecol. Econ. 70 (4), 617–626
- Mouysset, L., Doyen, L., Jiguet, F., 2012. Different policy scenarios to promote various targets of biodiversity. Ecol. Indicators 14 (1), 209–221.
- Mouysset, L., Doyen, L., Jiguet, F., 2013. How does economic risk aversion affect biodiversity? Ecol. Appl. 23 (1), 96–109.
- Mouysset, L., Miglianico, M., Makowski, D., Jiguet, F., Doyen, L., 2016. Selection of Dynamic Models for Bird Populations in Farmlands. Environ. Model. Assess. 407–418
- Ormerod, S.J., Watkinson, A.R., 2000. Editors' introduction: birds and agriculture. J. Appl. Ecol. 37 (5), 699–705.
- Peer, G., Dicks, and Visoncti 2014. EU agricultural reform fails on biodiversity, Science 334(6188).
- Pereira, H.M., Leadley, P.W., Proenca, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarres, J.F., Araujo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guenette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R., Walpole, M., 2010. Scenarios for Global Biodiversity in the 21st Century. Science 330 (6010), 1496–1501.
- Perry, A.L., 2005. Climate Change and Distribution Shifts in Marine Fishes. Science 308 (5730), 1912–1915.
- Pimm, S.L., Raven, P., 2000. Extinction by number. Nature 403 (6772), 843–845.
 Princé, K., Lorrillire, R., Barbet-Massin, M., Jiguet, F., 2013. Predicting the fate of French bird communities under agriculture and climate change scenarios. Environ. Sci. Policy 33 (Nov), 120–132.
- Robinson, S. K., Thompson III, F. R., Donovan, T. M., Whitehead, D. R., and Faaborg, J. 1995. Regional forest fragmentation and the nesting success of migratory birds, Science.
- Sekercioglu, C., Schneider, S., Fay, John, P., Loarie, S.R., 2008. Climate change, elevational range shifts, and bird extinctions. Conserv. Biol. 22 (1), 140–150.
- Steffan-Dewenter, Ingolf, Kessler, Michael, Barkmann, Jan, Bos, Merijn M., Buchori, Damayanti, Erasmi, Stefan, Faust, Heiko, Gerold, Gerhard, Glenk, Klaus, Gradstein, S., Robbert, et al., 2007. Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. Proc. Natl. Acad. Sci. 104 (12), 4973–4978.
- Stephens, P.A., Mason, L.R., Green, L.R., 2016. Consistent response of birds population to climate change on two continents. Science 352 (6281), 80–84.
- Stjernman, Martin, Green, Martin, Lindstrm, ke, Olsson, Ola, Ottvall, Richard, Smith, Henrik G., 2013. Habitat-specific bird trends and their effect on the Farmland Bird Index. Ecol. Indicators 24 (Jan), 382–391.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y., Erasmus, B., De Siqueira, M.F., Grainger, A., Hannah, L., et al., 2004. Extinction risk from climate change. Nature 427 (6970), 145–148.
- Verhulst, P.F. 1845. Recherches mathematiques sur la loi d'acroissement de la population.

 Nouveaux memoires de l'Academie Royale des Sciences et Belles-Lettres de Bruxelles.

 Whelan, C.J., Wenny, D.J., Marquis, R.J., 2008. Ecosystem Services Provided by Birds.

 Ann. N. Y. Acad. Sci. 1134 (1), 25–60.
- Whittingham, M.J., 2011. The future of agri-environment schemes: biodiversity gains and ecosystem service delivery: Editorial. J. Appl. Ecol. 48 (3), 509–513.
- World Wildlife Fund, 2016. Living Planet Report 2016. Risks and resilience in a new era.