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Relaxing the production-conservation trade-off: Biodiversity spillover in the bioeconomic performance of ecological networks

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ABSTRACT

Ecological networks (ENs) aim to accommodate production and conservation within landscapes by shaping the spatial scope of conservation policies based on ecological criteria. The environmental effectiveness of these networks has been extensively studied; however, it has rarely been linked to their economic cost. This paper investigates whether EN-based spatial targeting relaxes the production-conservation trade-off and, if so, what the processes underlying its performance may be. We design an EN at the national level (France), with common farmland birds defined as a conservation goal and grassland expansion defined as a conservation lever. A dynamic, mechanistic, ecological-economic model simulates policy scenarios up to 2050 with alternative targeting strategies, including the EN. The results reveal that EN targeting is almost twice as cost-effective as a nationally homogeneous policy and about as cost-effective as focusing on biodiversity reservoirs, but with higher biodiversity gains. These outcomes rely on higher initial bird abundance in targeted regions, as well as positive feedback and spillover supported by bird dispersal. However, the EN's superiority only appears in the medium term because of ecological inertia. These interdisciplinary insights on a tool from ecology and conservation biology echo policy needs for the design and implementation of sustainable landscape management strategies.

1. Introduction

Land use is at the center of conflicts between production and conservation objectives of agricultural and forestry landscapes (Faith et al., 1996; Klaseen et al., 2016; Smith et al., 2012). Public policies such as landscape planning (Kennedy et al., 2016), protected areas (Abarca et al., 2022), and agri-environmental schemes (Wätzold et al., 2016) have been proposed and implemented to ease this trade-off. However, biodiversity losses continue to occur in Europe (Bowler et al., 2019; Burns et al., 2021; Hallmann et al., 2017), questioning the environmental effectiveness and the cost-effectiveness of the public policies pursued so far (European Court of Auditors, 2017; Pe'er et al., 2020). As ambitious biodiversity targets have been set up for the decade at the European and global levels (Hermoso et al., 2022; Obura, 2023), ingenious landscape management strategies are needed to allow biodiversity

to thrive within production landscapes.

Ecologists and conservation biologists have introduced ecological networks (ENs) as an innovative tool to conciliate development and conservation by prioritizing environmental action based on ecological knowledge. Their origin lies in landscape ecology and metapopulation ecology, which study how landscape structure and dispersal affect species' spatial distribution and landscape resilience (Jongman, 2004). ENs enhance landscape connectivity: made up of biodiversity reservoirs (or core areas) linked by corridors, they facilitate demographic and genetic flows and, thus, species persistence (Baguette et al., 2013). From these ecological foundations, methodologies for identifying corridors and networks have been developed and applied from local to supranational scales (e.g., Cunha and Magalhães, 2019; DeMatteo et al., 2017; Jongman et al., 2011; Qian et al., 2023; Santos et al., 2018). Beyond demonstrating their environmental effectiveness (Gilbert-Norton et al.,

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2010; Liccari et al., 2022; Resasco, 2019), ENs and corridors have proven to function as “boundary objects”¹ between science and policy and have been integrated into numerous environmental policies (Lawton et al., 2010; Opdam et al., 2006; Ovaskainen, 2012; Van Der Windt and Swart, 2007; Wyborn, 2015).

In contrast, the bioeconomic performance of ENs (i.e., the joint impact on biodiversity and economic activity) remains unclear, as most evaluations solely focused on biodiversity gains or the provision of ecosystem services. Specifying the objectives and resources of landscape management yet requires an integrated understanding of the involved instruments (Smith et al., 2012), which calls for interdisciplinary investigation from modeling (Castro et al., 2018; Drechsler et al., 2022) to evaluation (Albers, 2022; Naidoo et al., 2006). In that respect, we can consider ENs as a specific form of spatial targeting, whose many economists push for as it improves cost-effectiveness in environmental land use policies (e.g., Bateman et al., 2015; Longo et al., 2021; Wünscher et al., 2008). Here, we ask whether EN-based spatial targeting can loosen the production-conservation trade-off within landscapes and examine the underlying spatiotemporal processes.

Apart from an illustrative and rudimentary cost-effectiveness analysis from Simberloff and Cox (1987), the few evaluations of ENs or corridors that have incorporated economic costs are relatively recent. We focus on *ex-ante* evaluations because they are appropriate for simulating and comparing options of spatial targeting. Previous works produced complementary knowledge, especially by applying different evaluation frameworks: cost-benefit (Newton et al., 2012), cost-effectiveness (Li et al., 2022; Lombard et al., 2010; Polyakov et al., 2023) or multi-criteria analyses (Newton et al., 2012; Théau et al., 2015). All, however, used static correlative modeling to simulate spatial targeting options (except for Polyakov et al. (2023), who used static mechanistic modeling). They generated landscape snapshots, assuming an equilibrium state for both economic actors and biodiversity, and biodiversity was assessed from a correlative relation between species and land cover (habitat suitability approach). Although this approach accounts for spatial heterogeneity, it neglects spatial dependence between biological populations and, consequently, the impact of landscape connectivity on biodiversity (Bauer et al., 2010). Moreover, the use of static modeling in these studies masks land use and biodiversity dynamics; however, these two dynamics can substantially affect the performance of conservation policies (Gregory and Beier, 2014; Zeller et al., 2020).

Building on previous literature, this work aims at evaluating the capacity of ENs to better conciliate conservation and production objectives when accounting for both spatial dependence and temporal dynamics. Moreover, it intends to untangle the mechanisms that underlie the EN's performance in this spatiotemporally explicit framework. These goals are addressed through a bioeconomic evaluation of an EN in an applied case with a mechanistic and dynamic modeling. Taking common farmland birds as a conservation goal and the expansion of permanent grasslands as a conservation lever in France, we simulate policy scenarios whose spatial scopes were specified from a predefined national EN. The ecological-economic model explicitly represents economic (land use choices) and ecological (bird metapopulation dynamics) processes. We specifically include bird dispersal to account for the influence of landscape structural organization in the resulting biodiversity status. The evaluation of the scenarios is performed with a cost-effectiveness analysis, completed by a multi-criteria ecological analysis. The resulting outcomes indicates that EN spatial targeting improves the cost-effectiveness of the conservation policy, and that its

relative performance depends on the time horizon. These outputs are not only due to a higher initial level of abundance in targeted regions but also to positive feedback and biodiversity spillover supported by bird dispersal. The multi-criteria framework discloses synergies and trade-offs between biodiversity indicators, which calls for arbitration.

The following sections are organized as follows: section 2 describes the modeling, simulation and evaluation frameworks, and the data used for calibration. Section 3 presents the main findings from a bioeconomic perspective at land use and bird abundance levels. Section 4 discusses the results and policy implications. Section 5 suggests research perspectives.

2. Materials and methods

2.1. The ecological-economic model

Figure 1 depicts the global structure of the ecological-economic model. On one side, a microeconomic model simulates land use choices based on profit maximization under a planning policy. On the other side, an agroecological model reproduces the metapopulation dynamics of biological species as a function of the ecological landscape. Land uses connect the economic and ecological parts of the model as an output of the microeconomic model and an input to the agroecological model.

For the microeconomic model, a regional land planner allocates surfaces of region r between land uses l each year t to maximize private profit:

$$\max_{S_{r,l}(t)} \Pi_r(t) = \sum_l \pi_{r,l} S_{r,l}(t) \tag{1}$$

where $S_{r,l}(t)$ is the regional area of land use l at year t and $\pi_{r,l}$ is the profit per unit of area of land use l . Land use profitability is spatially heterogeneous ($\pi_{r,l}$ varies across regions) but is held constant over area and time, assuming constant marginal productivity and price-taker land planners.

The available land area and past land distribution constrain the maximization program:

$$\sum_l S_{r,l}(t) = S_{tot,r} \tag{2}$$

$$\forall l, |S_{r,l}(t) - S_{r,l}(t-1)| \leq \xi_l * S_{r,l}(t-1) \tag{3}$$

where $S_{tot,r}$ is the regional total area and ξ_l is the flexibility parameter. Capping interannual land use variations, ξ_l captures the temporal inertia of the land that results from diverse technical, economic, or regulatory constraints. Public policies can be integrated within this economic program by modifying constraints (norms) or land use profitability (taxes, subsidies).

Regarding biodiversity, a metapopulation model represents a set of spatialized populations interacting. Ecological dynamics splits into intra-regional growth and inter-regional flows. Intra-regional growth follows a discrete Verhulst logistic growth:

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

where $N_{i,r}(t)$ is the abundance of the population of species i within region r at year t , $G_{i,r}(t+1)$ the abundance at year $t+1$ after intra-regional growth and before inter-regional flows, r_i the specific growth rate, and $K_{i,r}(t)$ the carrying capacity of region r at year t for species i . The carrying capacity is the population size the region can hold in the long term and accounts for intraspecific competition. This maximum population size depends on land use surfaces $S_{r,l}(t)$ and climate variables $C_{r,j}(t)$:

$$\frac{1}{K_{i,r}(t)} = \alpha_i + \sum_l \beta_{l,i} S_{r,l}(t) + \sum_j \gamma_{j,i} C_{r,j}(t) \tag{5}$$

¹ According to Wyborn et al. (2015), “boundary objects are artifacts, objects, or concepts that embody different meanings in scientific or non-scientific domains (Star and Griesemer, 1989). These things become boundary objects when used to mediate action across different social worlds (Bowker and Star, 2000; Star, 2010).”

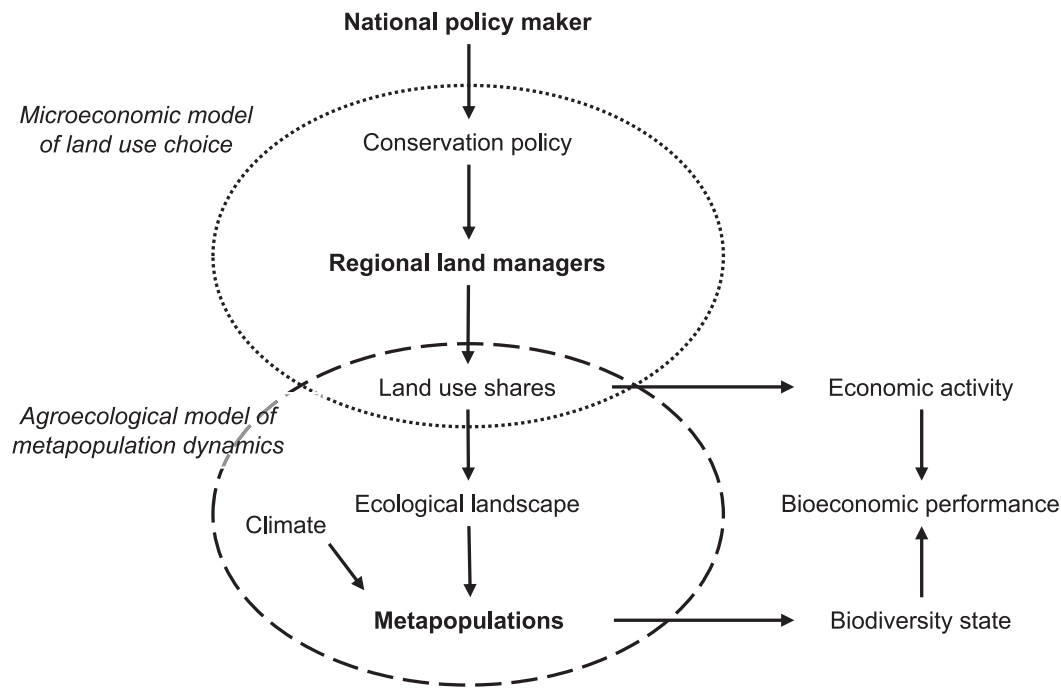


Fig. 1. Modeling framework.

where α_i captures specific fixed effects, $\beta_{l,i}$ assesses the response of species i to land use l , and $\gamma_{j,i}$ the response of species i to climate variable j . By expressing the carrying capacity $K_{i,r}(t)$ as the inverse of a linear expression, this functional specification allows for a linear relationship between the abundance $G_{i,r}(t + 1)$ and the land and climate variables $S_{r,l}(t)$, $C_{r,j}(t)$, appropriate for model estimation (see 2.2 and Appendix A5).

Then inter-regional flows link one region to the next with non-oriented dispersal so that the complete metapopulation dynamic is:

$$N_{i,r}(t + 1) = (1 - \tau_i)G_{i,r}(t + 1) + \tau_i \sum_n \frac{1}{m_n} G_{i,n}(t + 1) \quad (6)$$

with τ_i the specific dispersal rate, n the neighboring regions of r and m_n the number of neighbors of region n . As a first approximation, a fixed percentage τ_i of the population size after intra-regional growth disperses and equally splits into the neighboring regions. Neighboring is based on contiguity: two regions are neighbors if they share a common boundary.

2.2. Case study, data, and model calibration

2.2.1. Case study

The model applies to the French metropolitan territory, with birds chosen as the conservation target. We focus on birds because i) they have been well monitored over time (Jiguet et al., 2012), ii) are sensitive to environmental perturbations, directly or through food web (Bowler et al., 2019; Padoa-Schioppa et al., 2006), iii) provide ecosystem services (Whelan et al., 2008) and iv) are a major biodiversity conservation objective of environmental policies at multiple scales (EEA, 2019, chap. 3; ONB, 2022; Tittensor et al., 2014). Relying on the French Breeding Bird Survey (Jiguet et al., 2012), this case study covers 60 bird species, including 23 farmland specialists, 23 woodland specialists, and 14 generalist species.

Small Agricultural Regions (SARs) represent spatial units (regions r). These 707 homogeneous agricultural areas cover metropolitan France (excluding Paris) and vary between 0.1 and 44 km², with an average value of 8 km². An 8-item nomenclature describes their land use distribution (Table 1), and two climate variables (annual mean

Table 1

Land use classification. Land uses comprise internal dynamics (e.g., arable lands host a cultural system with rotations).

Code	Land use	Description
AL	Arable lands	Annual crops, leys and cultivated grasslands, fallow land
PC	Permanent crops	Vineyards, fruit trees and berry plantations, olive groves
GL	Grasslands	Pastures, meadows and other permanent grasslands under agricultural use
CA	Complex agricultural patterns	Mix of AL, PC or GL, without clear dominant cover
BF	Broadleaves forests	Forests with dominant deciduous species
CF	Coniferous forests	Forests with dominant coniferous species
MF	Mixed forests	Mix of BF and CF, without clear dominant cover
UR	Urban areas	Artificial surfaces (urban or industrial fabric...)

temperature and annual cumulative precipitations) their climate conditions. Because agricultural production and landscape are intertwined, and the size of SARs is of an order of magnitude consistent with bird dispersal capacity (Barbet-Massin et al., 2012; Paradis et al., 1998), SARs are also suitable units for bird metapopulation dynamics.

2.2.2. Data and model calibration

Calibrating the microeconomic and agroecological models relies on

Table 2

Data sources of variable and parameter values.

Variable / parameter	Data source
Bird abundance $N_{i,r}(t)$	French Breeding Bird Survey
Land use areas $S_{r,l}(t)$	CORINE Land Cover
Climate variables $C_{r,j}(t)$	MétéoFrance
Gross margins of agricultural land uses $\pi_{r,l}$	Regional Agricultural Accounts, French Annual Agricultural Statistics, Farm Accountancy Data Network, VisioNet (FranceAgriMer)
Gross margins of forestry land uses $\pi_{r,l}$	French Forestry Branch Survey, French Forestry Economic Observatory, CORINE Land Cover, French National Forestry Branch Accounts
Flexibility parameter ξ_i	Mouysset et al. (2019)

land use, production, climate, and biodiversity data (Table 2). Annual unit gross margins (revenue minus variable costs) account for agricultural and forestry land use yearly profits $\pi_{r,l}$. Though an imperfect proxy of the actual rent perceived by the landowner (e.g., only market production is captured), it is a good compromise between data availability and suitability as a decision criterion (e.g., Groot et al., 2007; Herzig et al., 2018; Jayet et al., 2023). Their assessment combines several sources of French public statistics for the years 2014–2018 (see Appendices A2 for procedure and A3 for resulting values). The values of the flexibility parameter ξ_i for the different land uses are those of Mouysset et al. (2019). They fixed these values “based on the ratios between land-use changes and related profits, [...] in order to ensure a realistic but flexible system” (Mouysset et al., 2019). Urban areas and permanent crops are stable over time ($\xi_i = 0$). For each bird species, a linear regression estimates the biological parameters of the agroecological model from data for the 2002–2019 period with the Within estimator (plm library of R software, version 4.1). Some constraints on the parameters are relaxed as a compromise between model fidelity, the goodness of fit and technical feasibility (Appendix A5). The resulting adjusted R^2 of the 60 estimated models varies between 0.63 and 0.95, with an average value of 0.83 (Appendix A6). See Appendix A for detailed method and results of model calibration.

2.3. Economic and ecological indicators

2.3.1. Economic indicator

Landscape economic production is evaluated through the national annual profit Π defined as follows:

$$\Pi(t) = \sum_r \sum_l \pi_{r,l} S_{r,l}(t) \tag{7}$$

which indicates the total economic value produced by agricultural and forestry land uses across the entire territory.

2.3.2. Bird abundance indicators

The Bird Abundance Indicators (BAIs) describe the overall trend of abundance of bird species groups using geometric averaging. They are declined according to species habitat preferences. As for the national Farmland Bird Index (FBI):

$$FBI(t) = \prod_f^F \left(\frac{N_{f,nat}(t)}{N_{f,nat}(t_0)} \right)^{1/F} \tag{8}$$

where base year $t_0 = 2002$, the first observation year of our dataset, $N_{i,nat}(t) = \sum_r N_{i,r}(t)$, f refers to farmland specialist species, and F to the number of farmland specialist species.

On the same pattern, the Woodland Bird Index (WBI) and the Generalist Bird Index (GBI) describe the abundance trend of the W woodland specialist species w and the G generalist species g :

$$WBI(t) = \prod_w^W \left(\frac{N_{w,nat}(t)}{N_{w,nat}(t_0)} \right)^{1/W} \tag{9}$$

$$GBI(t) = \prod_g^G \left(\frac{N_{g,nat}(t)}{N_{g,nat}(t_0)} \right)^{1/G} \tag{10}$$

BAIs (referred as Wild Bird Indicators in Gregory et al. (2005)) are regularly used to monitor biodiversity state and evaluate environmental policies (Fraixedas et al., 2020). They are therefore relevant “boundary object[s] at the interface between science and policy” (Heink and Kowarik, 2010).

2.3.3. Bird community indicators

Three community indicators account for structural features of bird communities. The Community Specialization and Trophic Indicators (CSI, CTI) reflect functional properties of bird communities. The first

step is to compute them at the regional scale:

$$CSI_r(t) = \sum_i \frac{N_{i,r}(t)}{N_{tot,r}(t)} SSI_i \tag{11}$$

$$CTI_r(t) = \sum_i \frac{N_{i,r}(t)}{N_{tot,r}(t)} \exp(STI_i) \tag{12}$$

where $N_{tot,r}(t) = \sum_i N_{i,r}(t)$ and SSI_i and STI_i are the Species Specialization Index and the Species Trophic Index of i . SSI_i values are the coefficients of variation of species abundance across 18 habitat categories (Julliard et al., 2006). The more a region r is occupied by habitat specialist species, the higher its CSI_r . STI_i values depend on species diet (Mouysset et al., 2012). The more a bird community is composed of high trophic level species (i.e., insectivorous or carnivorous, as opposed to low-trophic-level granivorous species), the higher its CTI_r . Appendix B reports the species habitat category (farmland, woodland, generalist), SSI and STI values.

The arithmetic average of the regional indicators weighted by the area of the SARs provides the national CTI and CSI. A high CSI indicates specialized communities spared from global biotic homogenization (Olden and Rooney, 2006). A high CTI reflects communities with high-level foodweb that provide diversified ecosystem functions and services (Dobson et al., 2006; Soliveres et al., 2016). However, high CSI and CTI also describe communities more sensitive to environmental degradation (Devictor et al., 2008; Julliard et al., 2004; Teillard et al., 2015).

Finally, the inverse Simpson index (ISI) summarizes the species diversity within the community assemblage:

$$ISI_r(t) = 1 / \left(\sum_i \left(\frac{N_{i,r}(t)}{N_{tot,r}(t)} \right)^2 \right) \tag{13}$$

The denominator estimates the probability of picking up two individuals from the same species within the local community r , $N_{i,r}(t)/N_{tot,r}(t)$ being the estimated probability of picking one individual of species i . The lower the denominator, the more diverse the community. Consequently, the higher its inverse, i.e., the inverse Simpson index, the more diverse the community. The ISI would equal species richness if each species were equally abundant. This indicator can thus be interpreted as an effective number of species or Hill number (Sommerfeld et al., 2008). The national ISI is the arithmetic mean of the regional iSI_r , weighted by area, expressing the average degree of evenness within local communities.

2.4. Ecological network and policy scenarios

We define a national EN that targets the conservation of farmland birds, a focal species group for biodiversity assessment in environmental policy (e.g., EEA, 2019; ONB, 2022) and scientific ecology as well (e.g., Butler et al., 2010; Doxa et al., 2010; Gregory et al., 2019). The network design follows a two-step protocol in line with current practices and theoretical foundations (Correa Ayram et al., 2016; Honeck et al., 2020), using the Graphab software (Foltête et al., 2021):

- We first select the reservoir SARs, i.e., SARs that contain high levels of our species of interest. While reservoir identification often involves species distribution models to extrapolate geographical distribution (Honeck et al., 2020), here we identify the reservoirs by directly computing the FBI since we benefit from a bird survey dataset covering the entire territory with a high spatial resolution (Jiguet et al., 2012). The 100 SARs with the highest mean FBI value for 2017–2019 constitute the reservoirs. The number of biodiversity reservoirs is arbitrarily set to 100 to cover a significant yet reasonable part of the territory.
- Second, corridor SARs connect the reservoir SARs according to the least cost path approach: the “travel cost” is minimized to favor

interpopulation flows, accounting for the habitat suitability of the crossed SARs (Honeck et al., 2020). Habitat suitability is here approximated by the share of permanent grasslands within SARs because farmland species are positively associated with grasslands (Bowler et al., 2019; Cerezo et al., 2011; Laiolo, 2005).

243 SARs form the emerging network, namely 100 reservoirs and 143 connecting SARs (Fig. 2). Based on this EN, four policy scenarios investigate alternative spatializations of the same conservation policy:

- scenario ALL - No spatial targeting: the entire territory is subject to the conservation policy.
- scenario NET - Network targeting: all SARs belonging to the ecological network are subject to the conservation policy.
- scenario RES - Reservoir targeting: only reservoir SARs are subject to the conservation policy.
- scenario COR - Corridor targeting: only corridor SARs are subject to the conservation policy.

A fifth Laissez-Faire scenario (L-F) supposes no conservation policy on the territory.

2.5. Simulation of policy scenarios

The model simulates land use and bird dynamics for each scenario from 2019 to 2050 with an annual time step. For the intervention scenarios (ALL, NET, RES, and COR), a norm applies on the permanent grasslands within the intervention perimeters introduced above (see 2.4). The choice of a normative instrument is motivated by the fact that it echoes real policy instruments (e.g., the strict ban on turning over permanent pastures in flood-prone areas and wetlands required by the European nitrate directive) as well as the environmental objectives of planning documents, formulated as norms would be (e.g., the French Regional Strategies for Planning, Sustainable Development, and Territorial Equality). Two rules constitute this simulated norm:

1. In the first year (2019), the grassland area of the targeted SARs doubles compared to 2018. The area gained from the other land uses (except urban areas and permanent crops) is prorated to their initial area.
2. In subsequent years, the SARs within the spatial scope of the policy scenarios cannot see their grassland area reduced.

Rule 1 may appear drastic, but it occurs as part of exploratory scenarios: they aim to grasp the potential for ecological gains depending on the degree of political ambition. An alternative norm that prohibits grassland losses was simulated (rule 2 only): although this regulation caused a substantial economic cost, it did not generate biodiversity benefits (results not shown). Rule 2 authorizes exchanges of grasslands within SARs, which is coherent with the current monitoring and control of permanent pastures at the regional level in France (French Ministry of Agriculture, 2021).

Because the study focuses on the impact of landscape changes, the climate is considered a contextual variable. In that respect, the climate variables are fixed at constant values for the entire projection period (average values over the 2015–2018 period), representing a stationary climate trajectory.

2.6. Evaluation of policy scenarios

We use the economic and ecological indicators introduced in 2.3. to compare the bioeconomic performance of the scenarios.

First, the national economic and ecological impacts of each intervention scenario are evaluated in the short (2030), medium (2040), and long (2050) terms using scenario Laissez-Faire as a baseline. This way, the cost-effectiveness of the intervention scenarios is estimated either in terms of habitat (grassland share) or biodiversity (FBI) gains:

$$CE_{sc}^{GL}(t) = \frac{S_{sc}^{GL}(t) - S_{L-F}^{GL}(t)}{|\Pi_{sc}(t) - \Pi_{L-F}(t)|} \tag{14}$$

$$CE_{sc}^{FBI}(t) = \frac{FBI_{sc}(t) - FBI_{L-F}(t)}{|\Pi_{sc}(t) - \Pi_{L-F}(t)|} \tag{15}$$

where $S_{sc}^{GL}(t)$, $\Pi_{sc}(t)$ and $FBI_{sc}(t)$ are respectively the grassland area (in percentage of total land area), the annual profit (in percentage of Laissez-Faire annual profit) and the FBI at year t for scenario sc . The numerator is the national ecological benefit, i.e., the difference in the ecological performance indicator between scenario sc and scenario Laissez-Faire at year t . The denominator is the national economic cost, i.e., the difference in annual profit between sc and Laissez-Faire at year t . The grassland cost-effectiveness CE_{sc}^{GL} and the FBI cost-effectiveness CE_{sc}^{FBI} respectively describe the ecological benefit per cost unit at habitat (or conservation mean) and biodiversity (or conservation goal) levels.

Second, the FBI gains are also computed for the targeted and untargeted SARs of the spatial-targeting scenarios (NET, RES, and COR), adapting eq. (8) to the corresponding spatial scopes. This decomposition exhibits the ecological impacts within and outside the scenarios' intervention area.

Finally, the five other ecological indicators (WBI, GBI, CSI, CTI, ISI) defined in eqs. (9)–(13) complete the evaluation with a multi-criteria analysis to check for possible side effects of the policy scenarios. The policy scenarios are then classified for every indicator according to their relative performance using the difference between the lowest and highest scenarios ("max-min range") in the medium term (2040). Poor performers are below 30% of the max-min range, high performers above 70% of the max-min range, and medium performers in-between. This categorization stresses the scenarios' strengths and weaknesses.

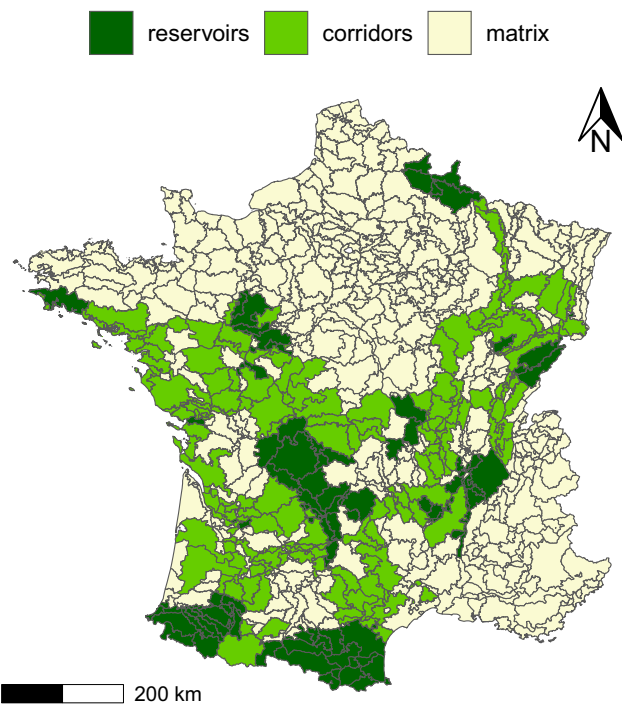


Fig. 2. The ecological network. It comprises 100 reservoir Small Agricultural Regions (SARs) selected according to their FBI value and 143 corridor SARs selected according to their grassland area.

3. Results

3.1. Land use distribution

Figure 3 presents the national land use distributions generated by policy scenarios for 2040. In the absence of grassland requirement (scenario Laissez-Faire), complex agricultural patterns and arable lands strongly increase (+10 points of area share compared to 2018 for arable lands, +8 for complex patterns) at the expense of grasslands (-4 points) and forest land uses (-9, -3 and -2 points for broadleaves, coniferous and mixed forests respectively). Indeed, the former are generally the most profitable land uses (Appendix A3). However, the constraint on inter-annual land use changes and the spatial heterogeneity of land use profitability maintain a diversified portfolio at the national scale.

In scenario ALL, grasslands strongly increase (+21 points compared to 2018), first because of the initial expansion shock combined with the restriction on grassland losses, and second because grassland locally shows higher profitability. Consequently, arable lands have their total area reduced (-4 points), the development of complex agricultural pattern is restrained (+1 points), and the decrease of forest is slightly larger (-11, -5, -2 points) compared to scenario Laissez-Faire. The spatial-targeting scenarios (NET, RES, and COR) show intermediate land use distributions: in line with the number of targeted SARs (243, 100 and 143, respectively for NET, RES and COR), the distribution is either closer to the one of ALL or the one of L-F. Overall, the differences in land use distribution result from the combined effects of the economically driven land use changes with the expansion norm.

Land use distributions in the short (2030) and the long (2050) terms broadly follow the one in 2040, with less or more divergence between scenarios according to the time spent since 2019 (Appendix C).

3.2. Grassland cost-effectiveness

Figure 4a shows the grassland cost-effectiveness CE^{GL} , i.e., the gain of grassland area per unit of lost profit for each intervention scenario. Scenario COR is the most cost-effective, followed by scenarios NET, ALL, then RES: in 2040, an economic loss of 1% of the profit of scenario L-F

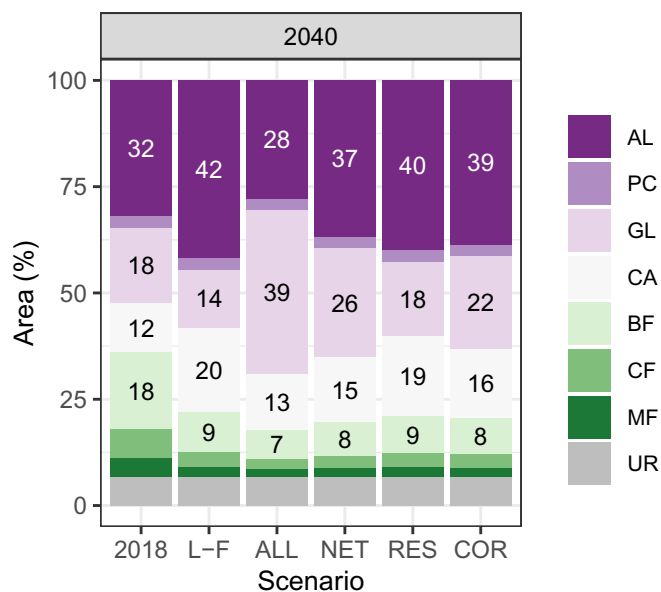


Fig. 3. National land use distribution of each policy scenarios by 2040. AL: arable lands; PC: permanent crops; GL: grasslands; CA: complex agricultural patterns; BF: broadleaves forests; CF: coniferous forests; MF: mixed forests; UR: urban areas. For the sake of clarity, national cover percentages are not printed on the figure for PC (3-3-3-3-3-3%), CF (7-4-2-3-3-3-3%), MF (4-2-2-2-2-2%) and UR (7-7-7-7-7-7%).

increases the national grassland cover by 2.3 points for COR, against 2.0, 1.8, and 1.5 points for scenarios NET, ALL, and RES. This ranking differs from the total cost ranking (Fig. 4b): expectably, and similarly to the national grassland cover, the greater the number of SARs affected by the norm, the higher the cost. In 2040, the yearly cost of a national norm (scenario ALL) is 13.6% of Laissez-Faire annual profit. Spatial targeting greatly reduces the cost, with 6.1, 2.7 and 3.5% of L-F annual profit in 2040 for scenarios NET, RES, and COR.

The ranking differences between grassland cost-effectiveness CE^{GL} and total cost highlight the spatial variability of grassland expansion's unit cost and how targeting strategies capture it. For instance, even though scenario COR is more expensive than scenario RES, its superior cost-effectiveness demonstrates a lower unit cost within its intervention area. The specification rules used to design the ecological network explain this gap. Corridor SARs are selected according to their share of grasslands, whereas the selection of reservoir SARs depends on the FBI. By targeting grassland-abundant SARs, scenario COR also targets SARs with more profitable grasslands on average: the mean gross margin is 570€/ha for corridor SARs against 310€/ha for reservoir SARs (mean weighted by SAR area). Conversely, arable lands are less profitable in corridor SARs (1120€/ha) than in reservoir SAR (1790€/ha). Thus, the cost of substituting one hectare of arable lands with grasslands is lower in corridor SARs, whose scenario COR targets, than in reservoir SARs, whose scenario RES targets. Because scenario NET combines scenarios RES and COR, it shows intermediate cost-effectiveness.

Over time, the grassland cost-effectiveness CE^{GL} decreases for all scenarios (Fig. 4a). It is even more true for the initially high-performing scenarios (COR and NET) so that the differences between scenarios gradually fade. This trend stresses how the annual cost of the conservation policy keeps increasing (Fig. 4b) while grassland expansion slows down.

3.3. FBI cost-effectiveness

Regarding the conservation goal, the intervention scenarios reveal contrasted FBI cost-effectiveness CE^{FBI} (Fig. 5a). In 2040, scenario NET is the most cost-efficient scenario (1.9 points of FBI gained per percentage of intervention cost), slightly overtaking RES (1.8) and more largely COR (1.5) and ALL (1.0). These performance differences expose the non-linearity between economic cost and the FBI benefit. The gain of FBI expectably increases with the extent of the intervention area of policy scenarios, from +4.9 points of FBI for scenario RES to +13.9 for scenario ALL in 2040 (Fig. 5b). However, while the ordinal relationship is similar to the one of the economic cost, quantitative differences engender the superior cost-effectiveness of spatial-targeting scenarios. Notably, although scenario NET is relatively expensive, it generates FBI benefits close to scenario ALL, rendering its superior cost-effectiveness.

The cost-effectiveness ranking at the FBI level also differs from the grassland level. Whereas scenario COR is the most cost-effective regarding grasslands in 2040, it is only the third regarding the FBI. On the contrary, scenario RES is the least cost-efficient scenario at the grassland level in 2040; at the FBI level, it is in second position after scenario NET.

In addition, unlike the grassland cost-effectiveness CE^{GL} , the FBI cost-effectiveness CE^{FBI} enhances over time. The rate of this trend is yet different between scenarios so that their ranking modifies over time. In 2030, the most cost-effective scenario is not NET but RES, and the cost-effectiveness of COR is closer to ALL. On the contrary, in 2050, the gap between scenarios NET and RES is wider than in 2040, and the cost-effectiveness of COR is closer to the other spatial-targeting scenarios.

3.4. Farmland bird dynamics

The FBI dynamics within and outside the intervention areas of the spatial-targeting scenarios explain the differences in FBI cost-

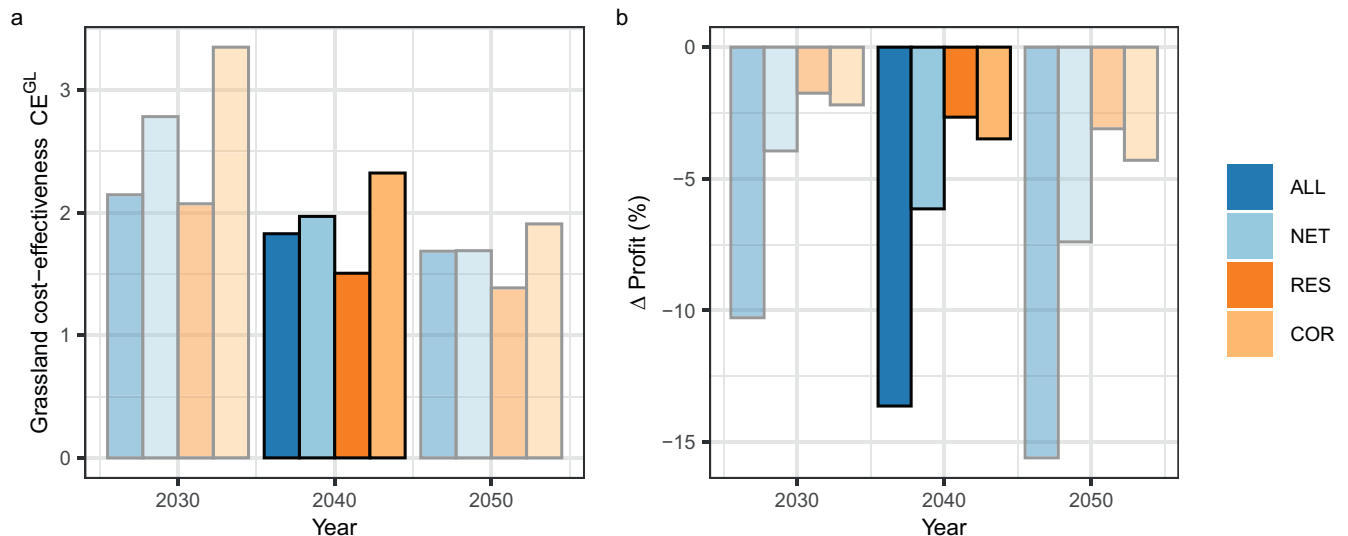


Fig. 4. Bioeconomic performance of public policy scenarios at habitat level. a) Grassland cost-effectiveness CE^{GL} of intervention scenarios, i.e., the gain of grassland area per cost unit; b) Cost of intervention scenarios. Gains and costs of scenarios are computed at short (2030), medium (2040) and long term (2050) with scenario Laissez-Faire for baseline. Grassland gains are in percentage points of the national surface. Costs are in percentage points of Laissez-Faire annual profit. Scenario ALL: norm applied to national territory; NET: ecological network targeting; RES: biodiversity reservoir targeting; COR: corridor targeting.

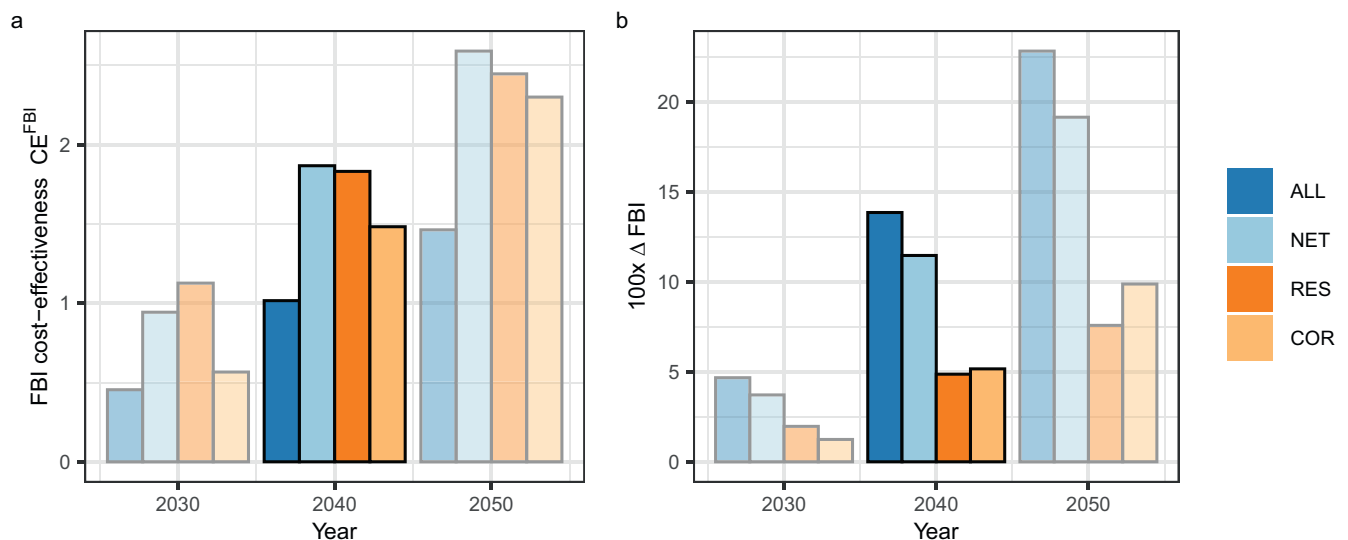


Fig. 5. Bioeconomic performance of public policy scenarios at biodiversity level. a) FBI cost-effectiveness CE^{FBI} of intervention scenarios, i.e., the gain of FBI points per cost unit; b) National gain of FBI points. Gains and costs of scenarios are computed at short (2030), medium (2040) and long term (2050) with scenario Laissez-Faire for baseline. FBI is in base 100 (base year = 2002). Costs are in percentage points of Laissez-Faire annual profit. Scenario ALL: norm applied to national territory; NET: ecological network targeting; RES: biodiversity reservoir targeting; COR: corridor targeting.

effectiveness CE^{FBI} (Fig. 6). For the three scenarios, the gain in FBI compared to Laissez-Faire increases over time *within* the set of targeted SARs (Fig. 6a). This expectable trend highlights the positive effect of grassland expansion on the intra-regional growth of bird populations within targeted SARs. The impact of the grassland expansion shock is yet gradual, pointing out ecological inertia.

Most importantly, scenarios show distinct dynamic behaviors. RES approximately follows a concave curve and COR a convex one. In other words, RES experiences higher benefits in the short term, but the gap between the two scenarios gradually reduces as the FBI growth of RES slows down and the one of COR accelerates. These contrasts are related to their targeting strategies. Intervening on SARs with high initial FBI, RES favors short-term gains before showing signs of habitat saturation. Focusing on grassland share, COR generates fewer and delayed benefits. Regarding scenario NET, it first has an intermediate dynamic between

RES and COR, congruent with combining the two. However, NET remarkably overtakes RES around 2035, revealing positive feedback beyond the additive effects of reservoirs and corridors.

More surprisingly, untargeted SARs also receives FBI gains (Fig. 6b), indicating that the conservation policy generates ecological benefits *outside* the intervention area. This biodiversity spillover follows a convex shape: negligible in the first decade, it develops a more substantial weight in the long term. This phenomenon especially concerns scenario NET, whose FBI positive spillover is approximately twice as high as RES and COR. This spillover comes from ecological dispersal: part of the population growth within prolific SAR is redistributed to the neighboring SARs so that the positive impact of the expansion norm spreads from one patch to the next.

In summary, RES has the highest ecological benefit in the short term thanks to its targeting strategy based exclusively on the biodiversity

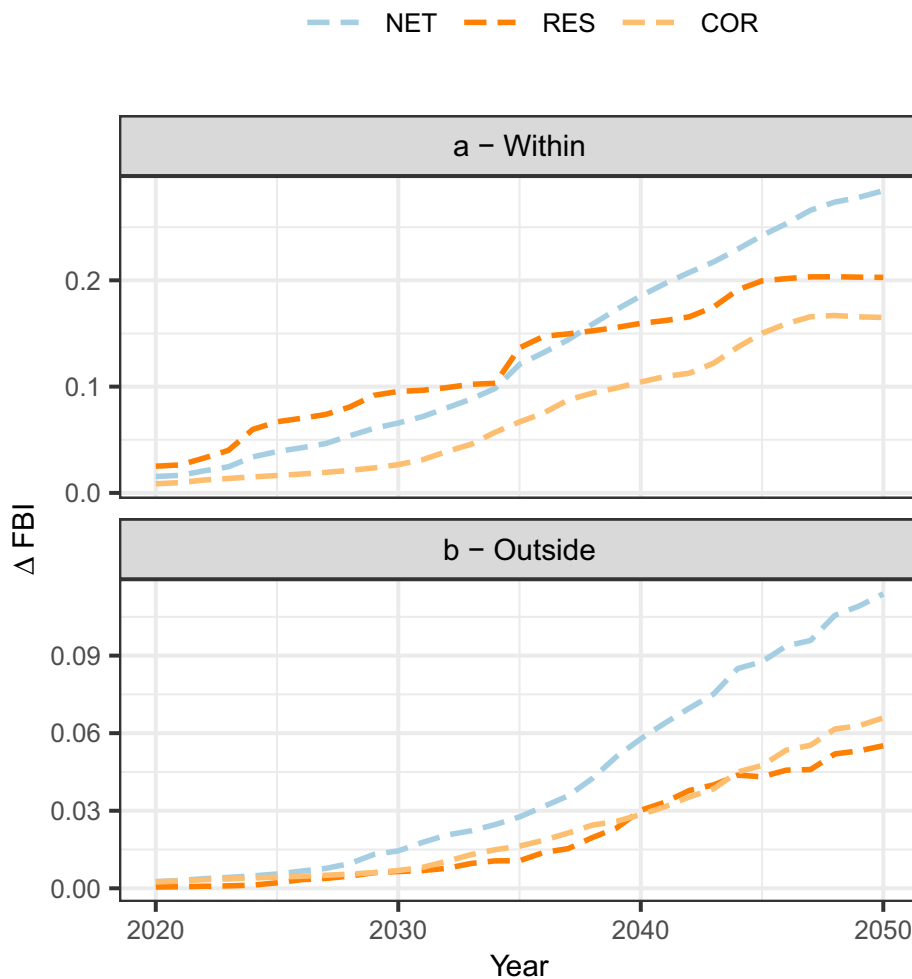


Fig. 6. FBI gain within (a) and outside (b) the intervention perimeter of spatial-targeting scenarios. The gain of FBI of scenarios NET, RES, and COR is defined in comparison to scenario L-F. The intervention perimeter of each scenario is their set of targeted SARs.

criterion and is, therefore, the most cost-effective. In the long term, NET benefits more from positive feedback and biodiversity spillover effects because it has a large and contiguous intervention area that supports dispersal. Thus, it becomes the most cost-effective. COR is penalized by a weak initial internal growth rate and continues to perform the worst, although it gradually closes the gap.

3.5. Ecological community analysis

Figure 7 shows the trajectories of the six ecological indicators for each policy scenario. The Bird Abundance Indicators, namely the FBI, the WBI, and the GBI (Fig. 7a-c), have qualitatively similar behaviors. First, all intervention scenarios produce ecological benefits compared to scenario L-F. Second, the divergence of the scenarios is progressive over time, reflecting the inertia of metapopulations to grassland expansion. Third, the ranking of scenarios roughly fits the spatial extent of the norm, except for scenarios RES and COR, which mostly have reversed ranking. Therefore, regarding population density, grassland development benefits all three species groups.

However, the Community Specialization Indicator (CSI) highlights that the benefit size differs between habitat groups (Fig. 7d). While the CSI decreases over time in scenario L-F, it increases in the intervention scenarios, to a moderate level for RES and COR, to the level observed in the 2000s for NET and ALL. Such a trend indicates that specialist species benefit more from grassland expansion than generalist species.

The Community Trophic Index (CTI) experiences more complex dynamics with non-monotonicity (Fig. 7e). Species dynamics are

asynchronous, with high or low trophic-level species alternately leading the indicator's dynamics. In addition, the relative position of the scenarios for this indicator repeatedly changes over time, making it difficult to determine an unambiguous effect of grassland expansion on community trophic structure.

Finally, unlike the Bird Abundance Indicators, the inverse Simpson index (ISI) decreases over time, especially for the intervention scenarios (Fig. 7f). In the case of scenario ALL, about 6 species-equivalents disappear between 2020 and 2050, 3.5 species more than in scenario L-F. Only the RES time series does not deviate much from L-F. Overall, while the abundance indicators reflect an overall positive trend, the ISI highlights the differential response of species to public policy so that evenness decreases, i.e., local bird communities become, on average, more homogeneous.

3.6. Bioeconomic performance: A multicriteria evaluation

Table 3 summarizes the performance of each policy scenario for 2040. Overall, there is no win-it-all scenario. The aggregated ranking would depend on the value placed on biodiversity relative to economic outcomes and the relative importance placed on each dimension within biodiversity. For instance, if biodiversity assessment limits to Bird Abundance Indicators, the most appropriate policy would be:

- ALL if biodiversity were given the highest priority, regardless of economic costs.

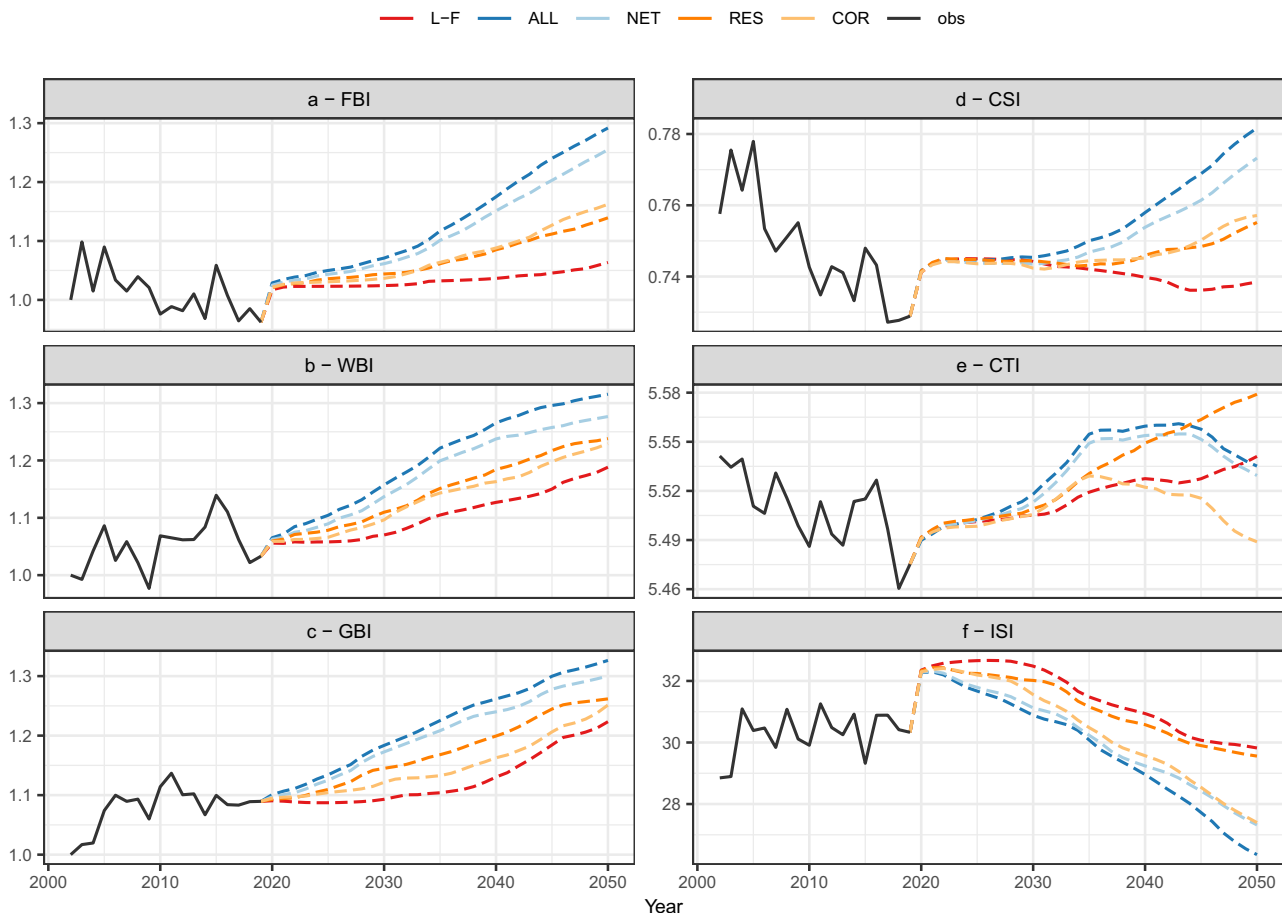


Fig. 7. Time series of the biodiversity indicators at national scale for each policy scenario. Scenario Laissez-Faire is considered a baseline, and the reader should focus on the gap between the intervention scenarios and Laissez-Faire. The jump in the first year of the simulation run (2020), common to all policy scenarios, must be seen as an artifact generated by model adjustment and is not given ecological significance.

Table 3

Multi-criteria performance of policy scenarios in 2040. Cells are colored by category of relative performance (light yellow: poor performer; light green: medium performer; dark green: high performer). Threshold values of performance levels are calculated from the “max-min range” (see 2.6).

	L-F	ALL	NET	RES	COR
<i>Cost</i>	0	13.6	6.14	2.66	3.48
<i>FBI</i>	1.04	1.18	1.15	1.09	1.09
<i>WBI</i>	1.13	1.27	1.24	1.18	1.16
<i>GBI</i>	1.13	1.26	1.24	1.20	1.16
<i>CSI</i>	0.740	0.758	0.754	0.746	0.745
<i>CTI</i>	5.53	5.56	5.55	5.55	5.52
<i>ISI</i>	30.9	29.0	29.2	30.6	29.6
<i>CE^{FBI}</i>		1.02	1.87	1.83	1.48

However, including indicators of community structure, ALL and NET may be unacceptable because of the steady decline in evenness of species distribution within SARs. RES would represent the best compromise.

4. Discussion

Four methodological features mark this work and allow us to comprehend the performance of ENs with an original angle. First, we integrate the economic cost of the simulated targeting strategies into the evaluation framework to assess their cost-effectiveness (Albers, 2022; Naidoo et al., 2006). Second, we use mechanistic ecological-economic modeling to reveal the processes underlying bioeconomic performance (Drechsler et al., 2022). Third, we use a dynamic framework to display the temporality of conservation policies (Castro et al., 2018). Finally, an ecological multi-criteria analysis investigates synergies and antagonisms between biodiversity dimensions (Mouysset et al., 2012). These methodological choices offer new insights that extend anterior bioeconomic results on ENs and lead to recommendations for conservation policy.

By simultaneously estimating ecological benefits and economic costs, we show in an applied case that ENs can improve the cost-effectiveness of conservation policies. Targeting EN greatly reduces opportunity costs compared to a homogeneous policy while producing high biodiversity benefits. In addition, this strategy is comparable with targeting only biodiversity reservoirs in terms of cost-effectiveness. Since the two targeting options present substantial differences in absolute impacts, discriminating between them is primarily a matter of ecological ambitions and allocated budgets, which is congruent with the conclusions of Polyakov et al. (2023). Overall, the results of the current

- NET if ecological ambitions were high and cost-effectiveness a consideration.
- RES in the case of a moderate environmental budget.

study indicate substantial room to direct conservation policy so as to generate biodiversity gains at a lower cost through a targeting strategy based on ecological criteria, including landscape connectivity. Policy-makers may reach such gains with popular instruments that have been spatially differentiated but do not necessarily incorporate connectivity (Guo et al., 2020). For instance, agri-environmental schemes can be made heterogeneous to fit existing EN like the French Green and Blue Belts. Agglomeration bonuses can also facilitate spatial coordination along an EN (Parkhurst and Shogren, 2007).

The integrated mechanistic modeling that connects land use choice with metapopulation dynamics (shown in Fig. 1) points out that the habitat cost-effectiveness does not reproduce the biodiversity cost-effectiveness. According to our modeling, habitat (grassland) cost-effectiveness is driven by economics via the spatial heterogeneity of opportunity costs. In contrast, the two ecological mechanisms of local population growth and dispersal are the leading channels of biodiversity (FBI) cost-effectiveness. Local population growth causes higher biodiversity gains in regions with initially abundant populations, and ecological dispersal generates a positive feedback loop and biodiversity spillover, respectively, within and outside targeted regions. Both mechanisms are consistent with patterns identified in empirical studies (Brudvig et al., 2009; Kleijn et al., 2006). Accounting for these complex ecological processes is thus essential for cost-effective conservation planning (Bauer et al., 2010; Hartig and Drechsler, 2009). In addition, we illustrate the limits of habitat indicators as proxies for biodiversity conservation. As these proxies are widely used by actual conservation policies, these limits demand caution in selecting indicators that best mirror conservation objectives (Simpson et al., 2022).

Highlighting the sensitivity of EN cost-effectiveness to ecological inertia, our time-explicit framework also adds up to anterior static evaluations that implied an immediate ecological response (Newton et al., 2012; Polyakov et al., 2023; Théau et al., 2015). In the short term, focusing on biodiversity reservoirs is the most cost-effective strategy. In the long term, EN-based spatial targeting outperforms the others. This difference of cost-effectiveness is because the weight of local growth and dispersal in the ecological dynamics vary over time and between spatial targeting strategies. Whereas ecological feedback and spillover effects are more pronounced in a continuous network, they are also subject to more inertia than local growth. As the strengths of ENs appear progressively, a long time horizon of policy evaluation is needed to capture their performance (Gregory and Beier, 2014).

Finally, the evaluation framework supplements the FBI with five other avian biodiversity indicators in order to reveal collateral effects. Although substitution of arable crops with permanent grasslands positively impacts generalist and forest specialist bird species, the global increase in abundance is associated with changes in community structure. The grassland expansion is more favorable to specialist species than generalists (Doxa et al., 2010; Princé et al., 2013), reversing the historical trend of replacement of habitat specialist species with generalist ones (Fontaine et al., 2020). Nevertheless, a lower species evenness at the sub-regional scale accompanies the differential impact of the norm on bird species. The absence of a “win-it-all” strategy requests weighting and arbitrating between non-aligned goals. In comparison with cost-benefit approaches that rely on a monetary estimation of ecosystem services (e.g., Newton et al., 2012), our combined cost-effectiveness and multi-criteria valuation framework does not aggregate the economic and ecological impacts of the EN. Such valuation approaches may be more suited to account for stakeholders' diverse values regarding biodiversity and support the formation of shared social values through deliberative processes (IPBES, 2022).

5. Research avenues

The insights presented above invite new pathways for research. Four developments in particular offer avenues to enhance the scientific credibility of policy-relevant knowledge on ENs (Cash et al., 2003).

One way in which this work might be extended is by checking the robustness for alternative model specifications, as a stylized model was applied as a first step. The economic module, for example, could incorporate diminishing marginal productivity and landowners' risk aversion (Mouysset et al., 2013). Both adjustments favor more diversified land use portfolios, which might reduce the opportunity cost of intervention scenarios compared to Laissez-Faire. Similarly to the statistical estimation of the ecological parameters, economic parameters could also be econometrically estimated to fit observation data better and assess the uncertainty of scenario outputs (Chakir and Le Gallo, 2013).

Contrasting ENs with optimal spatial targeting is another extension for research. Whereas this study focuses on the relative performance of ecology-based targeting strategies selected a priori, the reserve network design approach computes the spatial scope that maximizes biodiversity cost-effectiveness for a given budget (e.g., Jiang et al., 2007). By applying the two approaches, ENs and spatial optimums could be compared in terms of cost-effectiveness and intervention perimeter, informing on the ability of EN to approach optimal intervention (Dilkina et al., 2017). Such insights are especially relevant for conservation policies since ENs are well known to policymakers and less costly to define than optimized networks.

To better focus on spatial targeting, the model in this paper considers a reduced set of land use types from which the landowner constitutes their portfolio. This methodological choice implies that land management practices (e.g., farm input consumption) and land quality (e.g., the density of agroecological infrastructures) are homogeneous within a given land use type. However, these two variables are decisive determinants of the bioeconomic performance of agricultural and forestry landscapes (Haines-Young, 2009; Smith et al., 2012). They are also subject to ongoing conservation policies (e.g., in France, a pesticide reduction plan and hedgerow plantation programs). Thus, depending on the available data, one could refine the modeling by incorporating these factors as decision variables and ecological inputs, leading to the investigation of spatialized conservation strategies that mobilize current leverages.

Assessing the bioeconomic performance of ENs under climate change would be another relevant research direction. As a first approximation, our simulation framework assumes a stationary climate. However, the ongoing climatic change will affect the performance of ENs. On the one hand, ENs can help species to adapt to climate change by supporting range shifts (Schmitz et al., 2015). On the other hand, land use changes induced by climate change (Lungarska and Chakir, 2018) might threaten the networks' persistence (Bakker et al., 2015). While this paper addresses the ability of ENs to relax the ecological-economic trade-off for a stable climate, the dynamic framework mobilized here has the potential to test EN in our world's changing climate.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolecon.2023.107966>.

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