Agricultural Systems 168 (2019) 58–72

Contents lists available at ScienceDirect

Agricultural Systems

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

Trade-offs and synergies between livestock production and other ecosystem services

Francesco Accatino[a,*], Alberto Tonda[b], Camille Dross[a], François Léger[c], Muriel Tichit[a]

[a] UMR SADAPT, INRA, AgroParisTech, Université Paris-Saclay, 16 rue Claude Bernard, 75005 Paris, France
[b] UMR GMPA, INRA, Université Paris-Saclay, 1 av. Brétignières, 78850 Thireval-Grignon, France
[c] UMR SADAPT, AgroParisTech, INRA, Université Paris-Saclay, 16 rue Claude Bernard, 75005 Paris, France

ARTICLE INFO

Keywords:
Livestock production
Ecosystem service
Trade-off
Synergy
Grassland

ABSTRACT

One of the biggest challenges today is to satisfy an increasing food demand while preserving ecosystem services. Farming systems have a huge impact on land cover and land use, it is therefore vital to understand how land cover and land use allocation can promote synergies between food production and other ecosystem services. Livestock production has multiple interactions with other ecosystem services and can promote synergies especially in grasslands. We investigated the interactions between livestock production and other ecosystem services and explored strategies to soften trade-offs and enhance synergies. We considered four ecosystem services (livestock production, crop production, carbon sequestration, and timber growth) in France. We considered 709 land units covering a wide range of farming systems where both food production and other ecosystem services are provided. For each land unit, we built ecological production functions that are models measuring the statistical influence of driving variables (i.e. land cover, land use, pesticide expense, and climate) on the provision of ecosystem services. Using an optimization procedure, we studied the extent to which livestock production could be increased without reducing other ecosystem services and without increasing total pesticide expense. We found that a 20% increase in livestock production could be achieved by all farming systems in France under those general constraints. The 709 land units could be grouped based on similar combinations of increases or decreases in specific ecosystem services during the optimization. 48% of land units were specialised on food production, 24% were specialised on other ecosystem services, 16% were specialised on the mixed provision of food production and other ecosystem services, whereas the remaining 12% showed decrease or no change in all ecosystem services. Livestock production was either in trade-off or in synergy with the other ecosystem services. The trade-offs could be softened through intensified use of cultivated land and spatial segregation of livestock production. The synergies could be enhanced only through major grassland expansion.

1. Introduction

With the increasing size of the human population, the global food requirement is expected to rise abruptly by 2050 (Tilman et al., 2011; Kastner et al., 2012). In particular, rising incomes are expected to increase the global demand for animal products (Godfray et al., 2010; Thornton, 2010; Aleksandratos and Bruinsma, 2012; Mottet et al., 2017). The challenge will be to satisfy that demand while also protecting the environment (Sutherland et al., 2006; Ericksen et al., 2009). To help meet that challenge, the Millenium Ecosystem Assessment (MEA, 2005) recognised ecosystem services, the benefits that nature provides to human society, as fundamental components of sustainable development.

Several authors have pointed out that focusing on the production of a single ecosystem service can negatively affect the provision of other ecosystem services, because trade-offs exist (Bennett et al., 2009; Seppelt et al., 2013). Therefore, it is important to understand how food production is interrelated with other ecosystem services (Zhang et al., 2007; Power, 2010; Foley et al., 2011) in order to identify strategies to soften trade-offs and promote synergies (Dumont et al., 2013). Livestock production, in particular, has been recognised as having the potential to influence multiple ecosystem services (Herrero and Thornton, 2013). A recent study by Rodríguez-Ortega et al. (2014) reviewed the trade-offs and synergies between pasture-based livestock production and other types of ecosystem services at different spatial scales. They highlighted the need for new, more quantitative analyses of the

* Corresponding author.
E-mail addresses: francesco.accatino@inra.fr (F. Accatino), alberto.tonda@inra.fr (A. Tonda), camille.dross.2008@polytechnique.org (C. Dross), francois.leger@agroparistech.fr (F. Léger), muriel.tichit@inra.fr (M. Tichit).

https://doi.org/10.1016/j.agsy.2018.08.002
Received 7 February 2018; Received in revised form 5 July 2018; Accepted 2 August 2018
Available online 09 November 2018

linkages between pasture-based livestock production and other ecosystem services.

Farming systems are among the principal drivers of land cover and land use allocation and their total impact can profoundly transform land surface on a large scale (Lovell et al., 2010 and see the scenarios for Europe by Holman et al., 2017). These transformations are among the most important drivers of the anthropogenic effects on ecosystem services (Foley et al., 2005; Metzger et al., 2006; Tsonkova et al., 2015). Livestock production impacts both directly and indirectly on land use. The direct impacts correspond to the vast areas of pasture and grassland used for livestock grazing, while the indirect impacts correspond to feed production (Ramankutty et al., 2000). Roughly, at the global level, the 25% of agricultural land is dedicated to grazed land while about the 15% is used for forage crops (Ramankutty et al., 2000; Monfreda et al., 2008). Agricultural production causes trade-offs with other ecosystem services. Agricultural land expansion is the most important driver of ecosystem service losses (Foley et al., 2005). In addition, the intensification of land use for food and feed production negatively impacts on biodiversity and other ecosystem services (Hallmann et al., 2014; Teillard et al., 2016). Grasslands promote synergies between ecosystem services, because they can provide agricultural production as well as other ecosystem services (e.g. carbon sequestration [Soussana et al., 2004]) and biodiversity (Lemaire et al., 2005; Sabatier et al., 2015; Teillard et al., 2015; Dross et al., 2018). In addition, grassland would increase livestock production without using pesticides, which are, instead, used in fodder cultivation.

To better understand the relationships between livestock production and other ecosystem services, as well as identifying measures in farming systems to overcome the trade-offs, it is important to study the drivers of trade-offs and synergies between ecosystem services (Bennett et al., 2009; Rodríguez-Ortega et al., 2014). Correlation-based analyses (Chan et al., 2006; Jopke et al., 2014) and cluster analyses (Raudsepp-Hearne et al., 2010; Morelli et al., 2017) provide information about the co-occurrence of ecosystem services; however, they ignore the linkages to drivers, which must be understood in order to find management strategies that soften trade-offs and enhance synergies.

Optimization techniques are useful for studying the relationships among two or more ecosystem services (Groot and Rossing, 2011). They have been used to explore the trade-offs between contrasting objectives in Pareto frontiers (Groot et al., 2010; Groot et al., 2012), food production and biodiversity (Teillard et al., 2016; Dross et al., 2017, 2018), and economic return and biodiversity (Polasky et al., 2008). They have also been used to maximize one objective while imposing constraints of no-loss on other objectives (Butsic and Kuemmerle, 2015) and to systematically explore management variables and identify solutions (Seppelt et al., 2013). While some optimization scenarios were formulated for the trade-off between agriculture and biodiversity, a lower effort was put on the relationship between livestock production and other ecosystem services, implying that these relationships have been hypothesized theoretically but not explored in a more quantitative way with an optimization model.

We investigated the performance of a large set of alternative land cover and land use allocations across the whole of France, identifying trade-offs and synergies between livestock production and other ecosystem services. We explored strategies to soften the trade-offs and enhance the synergies. We hypothesized (following more qualitative studies [e.g., Rodríguez-Ortega et al., 2014]) that grasslands promoted synergies between livestock production and other ecosystem services with the additional advantage of increasing livestock production without increasing the use of pesticides. Our modelling approach served to provide quantitative information about the extent to which this could be achieved. Also, we quantified the extent to which conflicts among ecosystem services could be softened, considering the different constraints posed on land cover and land use change, and discuss the consequences of the strategies proposed by the model. We divided France in 709 land units, each of them corresponding to the spatial extension of a farming system. For each land unit, we built and calibrated with data ecological production functions (EPFs; Tallis and Polasky, 2011) that predicted the provision of four ecosystem services (i.e., livestock production, crop production, carbon sequestration, and timber growth) based on land cover, land use, and climatic variables. We used the EPFs to formulate a constrained optimization problem in which we sought to optimise total French livestock production while imposing constraints of no loss on the total provision of the other three ecosystem services.

2. Methods

We defined the set R of regions, being each region representative of the area of a farming system, corresponding to a set of farms in a particular geographic location (Giller, 2013). Within each region r, the management area A_r [ha] is defined as the portion of land containing different land covers that provide the ecosystem services considered in this study. We defined S as the set of ecosystem services. Being $s \in S$, we defined $w_{s,\ r}$ as the amount of ecosystem service s provided in the management area of the region r. The set S is formed by livestock production (LP) [$\mathrm{Mcal\,yr^{-1}}$], crop production (CP) [$\mathrm{Mcal\,yr^{-1}}$], carbon sequestration (CS) [$\mathrm{gC\,yr^{-1}}$], and timber growth (TG) [$\mathrm{m^3\,yr^{-1}}$]. Livestock production represents the sum of the energy contained in meat and milk products from ruminants (dairy and beef cattle, goats, and sheep). Altogether, those species contribute to 68% of the total French national protein production. We excluded pigs and poultry, because those species are more dependent on feed imports and are thus less related to the land than the ruminants. Carbon sequestration represents the flux of carbon subtracted from the atmosphere, which we assume to be a proxy for the capacity of the land cover to mitigate climate change. Timber growth represents the annual amount of timber produced by broadleaf and coniferous forests (Gallaun et al., 2010). Analogously to the set of ecosystem services, we also define the set M of environmental impacts, where, being $m \in M$, $w_{m,\ r}$ represents the amount of environmental impact m produced in the management area of region r. In this set, we only consider the pesticide expense PE, which represents the total amount of pesticide expense used for crop and fodder cultivation.

We defined a set D of decision variables. Being d the generic variable, the quantity $\theta_{d,\ r}$ represents the value of the decision variable d in the region r. A combination of values of all the decision variables in a region is denoted by $\times_{d \in D}\{\theta_{d,\ r}\}$ and provides a value $w_{s,\ r}$ of an ecosystem service s through a function $f_{s,\ r}(\times_{d \in D}\{\theta_{d,\ r}\})$ and a value $w_{s,\ r}$ of environmental impact m through a function $f_{m,\ r}(\times_{d \in D}\{\theta_{d,\ r}\})$ The optimization procedure starts from an actual combination of decision variables in all the regions, denoted by $\times_{d \in D, r \in R}\{\bar{\theta}_{d,r}\}$, corresponding to actual values of ecosystem services $\overline{w}_{s,r}$ in the different regions, explores different combinations of the decision variables in all the regions in order to find the optimal combination of decision variables $\times_{d \in D,\ r \in R}\{\theta_{d,\ r}{}^*\}$ corresponding to target ecosystem services $w_{s,\ r}{}^*$ and target environmental impact $w_{m,\ r}{}^*$ in the different regions.

In the optimization problem, we seeked to maximize the total livestock production in all the regions under some constraints.

$$\max\left(\sum_{r \in R} f_{LP,r}(\times_{d \in D}\{\theta_{d,r}\})\right) \tag{1}$$

With the constraints

$$\theta_{d,r} \in \Theta_{d,r}, \quad \forall\ d \in D, \forall\ r \in R \tag{2}$$

$$\sum_{r \in R} f_{s,r}(\times_{d \in D}\{\theta_{d,r}\}) \geq \sum_{r \in R} \overline{w}_{s,r}, \quad \forall\ s \in \{CP, CS, TG\} \tag{3}$$

$$\sum_{r \in R} f_{PE,r}(\times_{d \in D}\{\theta_{d,r}\}) \leq \sum_{r \in R} \overline{w}_{PE,r} \tag{4}$$

Eq. (1) represents the target optimization of livestock production at the whole national scale (it is the sum of the livestock production in all

Table 1
List of symbols and definitions.

Symbol	Unit	Mathematical definition	Description
Basic elements			
R	–		Set of the 709 SARs considered in France
S	–	$S = \{LP, CP, CS, TG\}$	Set of the ecosystem services
M	–	$M = \{PE\}$	Set of the environmental impact
D	–	$D = \{FOD, C, NPG, PG, F, p_{FOD}, p_C\}$	Set of the decision variables
L	–	$L = \{FOD, C, NPG, PG, F\}$	Set of the land cover fractions
Z_l	–		Set of the sub-fractions of the land cover l
U	–	$U = \{p_{FOD}, p_C, k\}$	Set of the land-use-related production factors
C	–	$C = \{P, T\}$	Set of the climate-related production factors
G	–		Set of the groups of SARs
R_g	–		Set of the SARs belonging to group g
A_r	ha		Management area of the SAR r
$w_{s,\ r}$, $\overline{w}_{s,r}$, $w_{s,\ r}{}^*$	–	Eq. (5)	Generic, initial, optimized value of the ecosystem service s in the SAR r
$w_{m,\ r}$, $\overline{w}_{m,r}$, $w_{m,\ r}{}^*$			Generic, initial, optimized value of the environmental impact m in the SAR r
$\theta_{d,\ r}$, $\overline{\theta}_{d,r}$, $\theta_{d,\ r}{}^*$	–		Generic, initial, optimized value of the decision variable d in the SAR r
$\theta_{l,\ r}$	–		Generic value of the land cover fraction l in the SAR r
$\theta_{l,\ z,\ r}$	–		Generic value of the sub-fraction z of the land cover fraction l in the SAR r
$\theta_{u,\ r}$	–		Generic value of land-use-related production factor u in the SAR r
$\theta_{c,\ r}$	–		Generic value of climate-related production factor c in the SAR r
$\Theta_{d,\ r}$	–		Set of the constraints posed on the decision variable d in SAR r
Ecosystem services and environmental impacts			
LP	[Mcal yr^{-1}]		Annual livestock production
CP	[Mcal yr^{-1}]		Annual crop production
CS	[gC yr^{-1}]		Annual carbon sequestration
TG	[m^3 yr^{-1}]		Annual timber growth
PE	[€ yr^{-1}]		Annual pesticide expense
Land cover fractions			
FOD	fraction		Fraction of the management area occupied by fodderland
C	fraction		Fraction of the management area occupied by cropland
NPG	fraction		Fraction of the management area occupied by non-permanent grassland
PG	fraction		Fraction of the management area occupied by permanent grassland
F	fraction		Fraction of the management area occupied by forest
Land cover sub-fraction			
$PG_{(231)}$	fraction		Fraction of the permanent grassland occupied by *Pastures* (CLC 231)
$PG_{(321)}$	fraction		Fraction of the permanent grassland occupied by *Natural Grasslands* (CLC 321)
$F_{(311)}$	fraction		Fraction of the forest occupied by *Broad Leaved Forest* (CLC 311)
$F_{(312)}$	fraction		Fraction of the forest occupied by *Coniferous Forest* (CLC 312)
$F_{(313)}$	fraction		Fraction of the forest occupied by *Mixed Forest* (CLC 313)
$F_{(323)}$	fraction		Fraction of the forest occupied by *Sclerophyllous Vegetagion* (CLC 323)
$F_{(324)}$	fraction		Fraction of the forest occupied by *Transitional Woodland-Shrub* (CLC 324)
Land-use-related production factors			
p_{FOD}	[€ ha^{-1} yr^{-1}]		Annual pesticide expense per unit area of fodderland
p_C	[€ ha^{-1} yr^{-1}]		Annual pesticide expense per unit area of cropland
k	[Mcal]		Average energetic content of cultivated crop
Climate-related production factors			
P	[mm yr^{-1}]		Mean annual rainfall
T	[°C]		Mean annual temperature
Cobb-Douglas function parameters			
$\alpha_{s,\ l,\ z}$	–		Coefficient of the Cobb-Douglas function referred to ecosystem service s and the sub-fraction z of the land cover fraction l
$\gamma_{s,\ u,\ l,\ z}$	–		Exponent of the Cobb-Douglas function referred to ecosystem service s, land-use-related production factor u, and the sub-fraction z of the land cover fraction l
$\gamma_{s,\ c,\ l,\ z}$	–		Exponent of the Cobb-Douglas function referred to ecosystem service s, land-use-related production factor c, and the sub-fraction z of the land cover fraction l
Parameters for the analysis of the results			
$\Delta w_{s,\ r}$	–	Eq. (7)	Variation of ecosystem service s per unit of management area in the SAR r.
$\widetilde{\Delta w}_{s,r}$	–	Eq. (8)	Normalised variation of ecosystem service s per unit of management area in the SAR r.
Δf_r	–	Eq. (9)	Index of change in food-related ecosystem services in the SAR r.
Δe_r	–	Eq. (10)	Index of change in ecosystem services (other than food-related ecosystem services) in the SAR r.
$\Delta w_{s,\ g}$	–	$\Delta w_{s,g} = \frac{\sum_{r \in R_g} \Delta w_{s,r}}{\sum_{r \in R_g} A_r}$	Variation of ecosystem service $s \in S$ per unit of management area in the group $g \in G$.
$\widetilde{\Delta w}_{s,g}$	–	$\widetilde{\Delta w}_{s,g} = \frac{\Delta w_{s,g}}{\max_{g \in G}(abs(\Delta w_{s,g}))}$	Normalised variation of ecosystem service $s \in S$ per unit of management area in the group $g \in G$.
$\Delta\theta_{l,\ g}$	Fraction	$\Delta\theta_{l,g} = \frac{\sum_{r \in R_g}((\theta^*_{l,r} - \overline{\theta}_{l,r}) \cdot A_r)}{\sum_{r \in R_g} A_r}$	Change of the land cover fraction l in the group g
$t_{PE,\ l,\ g}$	[€ m^{-2} yr^{-1}]	$t_{PE,l,g} = \frac{\sum_{r \in R_g}(\theta_{p_l,r} \cdot \theta_{l,r} \cdot A_r)}{\sum_{r \in R_g} \theta_{l,r} \cdot A_r}$	Annual Pesticide expense per unit area of land cover fraction $l \in \{C, FOD\}$ in the group g
$\Delta t_{PE,\ l,\ g}$	[€ m^{-2} yr^{-1}]	$t^*_{PE,l,g} - \bar{t}_{PE,l,g}$	Variation in Annual pesticide expense per unit area of land cover fraction $l \in \{C, FOD\}$ in the group g

regions). Eq. (2) represents the constraints posed on decision variables themselves. By definition, decision variables are included in some ranges, however there are additional region-specific constraints denoted by $\Theta_{d,\ r}$. Eq. (3) describes the constraint of no-loss on the ecosystem services other than livestock production: the total provision of those ecosystem services at the national level should not be lower than the one corresponding to the initial configuration of the decision variables. The last constraint (Eq. (4)) indicates that the total pesticide expense in the optimized configuration cannot be greater than the total pesticide expense corresponding to the initial configuration. Table 1 summarizes all notations used in our modelling framework.

2.1. Application to France

2.1.1. Formulation of the ecological production functions for ecosystem services

We applied the optimization model to France. As regions, we considered the Small Agricultural Region (SAR), that are elementary land units in France homogeneous in climate and soil (Klatzmann, 1995), containing land covers for both provisioning and regulating ecosystem services and approximating the area of a farming system. SARs have been successfully used in several studies of food production and biodiversity modelling (e.g. Mouysset et al. (2011), Princé et al. (2013), and Teillard et al. (2016)). In France, there are 714 SARs with an average area of 669.6 km^2. We considered in our study 709 SARs, specifically excluding Paris and the four SARs around Paris, which are highly urbanized.

For calculating the provision of ecosystem services we defined EPFs starting from land cover, land use, and climate variables. We assumed that each land cover fraction provides a certain amount of ecosystem services according to a Cobb-Douglas function, where different production factors correspond to land use and climate variables. Considering that a process-based model was too complicated to formulate and calibrate, we opted for a statistical model that could be calibrated with data. A Cobb-Douglas function, being a weighted product of production factors, provides a limited amount of substitutability between production factors, differently from a linear combination that would assume complete substitutability. The Cobb-Douglas function is furthermore widely used as a simple but efficient model in economy, with application in pure ecology (Barbier, 2007) or in economic-ecologic applications (Boumans et al., 2002; Onofri et al., 2017).

We defined L as the set of land cover fractions, U as the set of the land-use-related production factors, and C as the set of climate-related production factors. Each element l of the land cover fraction is associated to a set Z_l of fraction into which it is sub-divided. The values associated to elements of Z_l sum up to 1 for each l. The generic formulation of the EPF for the ecosystem service s in the SAR r is described by:

$$w_{s,r} = A_r \sum_{l\in L}\sum_{z\in Z_l} \alpha_{s,l,z}\cdot\theta_{l,r}\cdot\theta_{l,z,r}\cdot\left(\prod_{u\in U}\theta_{u,r}{}^{\gamma_{s,u,l,z}}\prod_{c\in C}\theta_{c,r}{}^{\gamma_{s,c,l,z}}\right) \tag{5}$$

See Table 1 for the detailed descriptions of the elements in the equations. Parameter $\alpha_{s,\ l,\ z}$ is a coefficient specific to the ecosystem service s, and to the sub-fraction z of the land cover l. Parameter $\gamma_{s,\ u,\ l,\ z}$ is the exponent of the land-use-related production factor u, specific to the ecosystem service s and to the fraction z of the land cover l. Parameter $\gamma_{s,\ c,\ l,\ z}$ is the exponent of the climate-related production factor u, specific to the ecosystem service s and to the fraction z of the land cover l. The coefficients of the land uses as well as the exponents of the production factors represent the parameters of the Cobb-Douglas function, are independent of the SAR and are parameterized with data following the procedure described in Section 2.1.7.

The set L of land cover variables is formed by fodderland FOD (arable land supporting livestock feeding), cropland C (arable land supporting crops for human consumption), non-permanent grassland NPG, permanent grassland, and forest F. The values associated to these variables in the SAR r, $\theta_{l,\ r}$, represent fractions of the management area A_r, they range between 0 and 1, and they sum up to one. The land cover fractions FOD, C, NPG are not sub-divided into fractions, therefore the set of their sub-fractions is formed by one element with value equal to 1. Land cover fraction PG is composed by two sub-categories $PG_{(231)}$ and $PG_{(231)}$, namely (following the Corine Land Cover [CLC] nomenclature (EEA, 2013)) *Pasture* (CLC category 231, put in subscript) and *Natural Grassland* (CLC 321), respectively. Land cover fraction F is composed by five sub-categories, namely *Broad Leaved Forest* (CLC 311), *Coniferous Forest* (CLC 312), *Mixed Forest* (CLC 313), *Sclerophyllous Vegetation* (CLC 323), and *Transitional Woodland-Shrub* (CLC 324), respectively.

The set of land-use-related production factors, U, is formed by the annual pesticide expense [€ $ha^{-1}\ yr^{-1}$] per unit area of fodderland and cropland, p_{FOD} and p_C, representing farm intensity (Teillard et al., 2012), as well as the production factor k [Mcal], which represents the average crop energetic content in the cropland fraction. Such a production factor is a proxy of the crop associations in the different parts of the country. We denote by $\theta_{u,\ r}$, $u \in U$, their values in the SAR r. The set of climate-related production factors, C, is formed by average annual precipitation P [mm yr^{-1}] and average annual temperature T [°C]. We denoted by $\theta_{c,\ r}$, $c \in C$, their values in the SAR r.

2.1.2. Formulation of the function for the environmental impact

The total expense in pesticide [€ yr^{-1}] in the SAR r constitutes an output of the model and is obtained with this formula:

$$w_{PE,r} = (\theta_{FOD,r}\theta_{p_{FOD},r} + \theta_{C,r}\theta_{p_C,r})A_r \tag{6}$$

2.1.3. Definition of the decision variables

As decision variables we choose all the land use fractions of set L (FOD, C, NPG, PG, F) and the annual pesticide expenses per unit area of cropland and fodderland (p_{FOD} and p_C). The elements not chosen as decision variables (k, T, P and the sub-fractions of PG and F) were kept constant along the optimization procedure and are therefore considered as parameters of the model. The choice of keeping k constant, corresponds to the assumptions that crop associations in the different SARs are the result of historic optimization given the local pedo-climatic conditions (Heck et al., 2018). The choice of keeping climate-related production factors constant translates that climate variables are characteristics of the SARs, as well as the management area. By considering as constants the sub-fractions of PG and F, we reduced the number of decision variables involved in the optimization process while still accounting for the contribution of a larger number of land cover types in the provision of ecosystem services.

2.1.4. Constraints on the decision variables

We posed SAR-specific constraints on the decision variables, defining the set $\Theta_{d,\ r}$ of Eq. (2). These constraints were posed for three reasons: (1) the model being calibrated for France, the decision variables cannot go outside the data used for model calibration; (2) the decision variables cannot be too different from the historic land cover or land uses in the different parts of France, in order to avoid unrealistic solutions; (3) there are biophysical and political constraints in the different parts of France. Details about the constraints on decision variables are described in Appendix 1. Constraints did not made changes possible in cropland and fodderland mostly in pastoral and mountain areas (14.5% of SARs), they did not made change possible in forest in 15% of the SARs, however they still enabled considerable expansion and reduction of land covers in different parts of the country and at the whole country level. At the French level, the total forest area could vary between −2% and + 5% of its actual value, the total grassland area could change between −16% and + 46% of its actual value and the other land uses could change at least between −41% and + 29% of their actual value. The total pesticide expense at the French level in cropland and fodderland could change between at least −53% and + 48% of its actual value.

2.1.5. Optimization procedure

The optimization problem was non-linear, with a considerable number of constraints on each decision variable. Therefore, we used an optimization technique based on an evolutionary algorithm (De Jong, 2006), which is the most suitable to escape local optima. The evolutionary algorithms do not always find the local optimum, however they can explore efficiently the space of the solutions and provide a first quantitative assessment of how livestock production could be increased in the respect of the constraints. Finding the exact optimum was out of our purpose. With a sub-optimal solution we were able to analyse how decision variables were changed and to discuss land cover and land use techniques for addressing trade-offs and synergies between ecosystem services. Evolutionary algorithms have been used previously in land use models (Teillard et al., 2016; Groot et al. (2010); see also Memmah et al. (2015) and the methodological paper of Groot and Rossing (2011)). The procedure is based on a state-of-the-art optimiser, the Covariance Matrix Adaptation Evolution Strategy (CMA-ES; Hansen and Ostermeier, 2001), implemented in Python. We chose that algorithm for its efficiency in tackling non-convex problems and the ease with which user-defined constraints can be introduced into the objective function.

2.1.6. Data

We used existing data to calibrate parameters of the EPFs (Eq. (5)) and to initialise the optimization procedure at the national level. We used existing data to obtain values for the land use fractions and sub-fractions, the land-use-related and the climate-related production factors (model inputs) and for the ecosystem services (model outputs). We focused on data from 2006, because that was the year for which the most data were available for the variables. We took a few datasets from different years, because data for some variables were unavailable for 2006.

We computed the areas dedicated to cropland, fodderland, non-permanent grassland, and permanent grassland in each SAR based on annual agricultural statistics (*statistiques agricoles annuelles*; Dross et al., 2017). We estimated the fraction of forest in each SAR, as well as the sub-fractions of forest and permanent grassland based on the CLC layers (EEA, 2013). We extracted rainfall and temperature data from the dataset of Haylock et al. (2008). We obtained the energetic content of the crops in the SARs from Dross et al. (2017). For the pesticide expense in the cropland and fodderland, we used the data set estimated by Butault et al. (2010) for 2006.

We obtained data of 2006 for crop and livestock production at the SAR level from Dross et al. (2017). For carbon sequestration and timber growth, we used layers fully described in Maes et al. (2011). The carbon sequestration layer consisted of a 1 km^2 × 1 km^2 grid that Veroustraete et al. (2002) produced to model carbon sequestration starting from the Normalised Difference Vegetation Index (NDVI). The timber growth layer came from the work of Gallaun et al. (2010), which combined national forest inventory data and remotely sensed vegetation data (MODIS).

2.1.7. Model calibration

We calibrated the parameters $\alpha_{s,\,l,\,z}$, $\gamma_{s,\,u,\,l,\,z}$ and $\gamma_{s,\,c,\,l,\,z}$ for the EPF dedicated to each ecosystem service. The calibration procedure was computed with CMA-ES (Hansen and Ostermeier, 2001), implemented in Python, minimizing the sum of the differences in the different SARs between measured and modelled ES. The optimization procedure included expert-assessed constraints on the relative values of the parameters in order to ensure that the model was realistic (e.g., the carbon sequestrated by a unit of forest area unit should be greater than that sequestrated by a unit of cropland). Because the calibration was done with the values of the land use variables corresponding to the initial configuration, applying Eq.(5) using the values $\bar{\theta}_{d,r}$, the values $\overline{w}_{s,r}$are obtained, for each decision variable d, SAR r, and ecosystem services s. No relationships were imposed a-priori between the parameters. For the ecosystem services, only the relationships depicted in Fig. 1 were considered (where the arrow is absent between the variable and the ecosystem service, the coefficient was not estimated but was instead set to zero). The parameter and R^2 values are shown in Table 2. In all the land covers, for livestock production, carbon sequestration and timber growth, the sum of the exponents of the Cobb-Douglas function was lower than one, indicating a decreasing return to scale, i.e., the ecosystem services increased less than linearly with the production factors considered. The only exponents showing an increasing return to scale was the crop association parameter. Crop production increased more than linearly with crop composition, indicating that highly productive crops can be in synergy and increase the total yield.

2.2. Analysis of the optimization results

We divided the SARs into groups that were homogeneous for the signs of the changes registered in the values of the different ecosystem services during the optimization procedure (Section 2.2.1). Within each group, we analysed the changes in the drivers causing the variation in ecosystem services (Section 2.2.2).

2.2.1. Grouping of the SARs based on similar changes in ecosystem services

We normalised the increases or decreases in ecosystem services in the different SARs. For each SAR r, we calculated the change in the value of each ecosystem service per unit of management area:

$$\Delta w_{s,r} = \frac{(w^{*}_{s,r} - \overline{w}_{s,r})}{A_r} \tag{7}$$

We then normalised the ecosystem service provision as follows:

$$\widetilde{\Delta w}_{s,r} = \frac{\Delta w_{s,r}}{\max\limits_{r \in R}(abs(\Delta w_{s,r}))} \tag{8}$$

The normalisation produced values ranging from −1 to 1, maintaining the positivity or negativity of the changes in the values of ecosystem services provided.

We then grouped the SARs according to the signs of the changes in the provision of the different ecosystem services. Because pairwise comparisons are easy to interpret and represent (Jopke et al., 2014), we followed a decision tree (depicted in Fig. 2) making successive pairwise comparisons. First, we grouped the four ecosystem services into two indices, one representative of food production, being it the maximum between the normalized variation of livestock production and crop production (Eq. (9)), and one representative of the other ecosystem services, being it the maximum between the normalized variation of carbon sequestration and timber growth (Eq. (10)).

$$\Delta f_r = \max(\widetilde{\Delta w}_{LP,r}, \widetilde{\Delta w}_{CP,r}) \tag{9}$$

$$\Delta e_r = \max(\widetilde{\Delta w}_{CS,r}, \widetilde{\Delta w}_{TG,r}) \tag{10}$$

If the index was negative, then both ecosystem services composing the index had a negative change; if the index was positive, at least one of the two ecosystem services composing the index had a positive change, and further investigation was necessary to identify which ecosystem service s had a positive change (see Fig. 2).

Second, we classified the SARs according to the combined signs of the two indices. If $\Delta f_r > 0$ and $\Delta e_r \le 0$, then the changes in carbon sequestration and timber growth were both negative (or null), so we explored the possible sign combinations of the changes in livestock production and crop production (they could be both positive or sign-discordant). If $\Delta f \le 0$ and $\Delta e > 0$, then the changes in livestock production and crop production were both negative (or null), so we explored the possible sign combinations of the changes in carbon sequestration and timber growth. If $\Delta f > 0$ and $\Delta e > 0$, then we

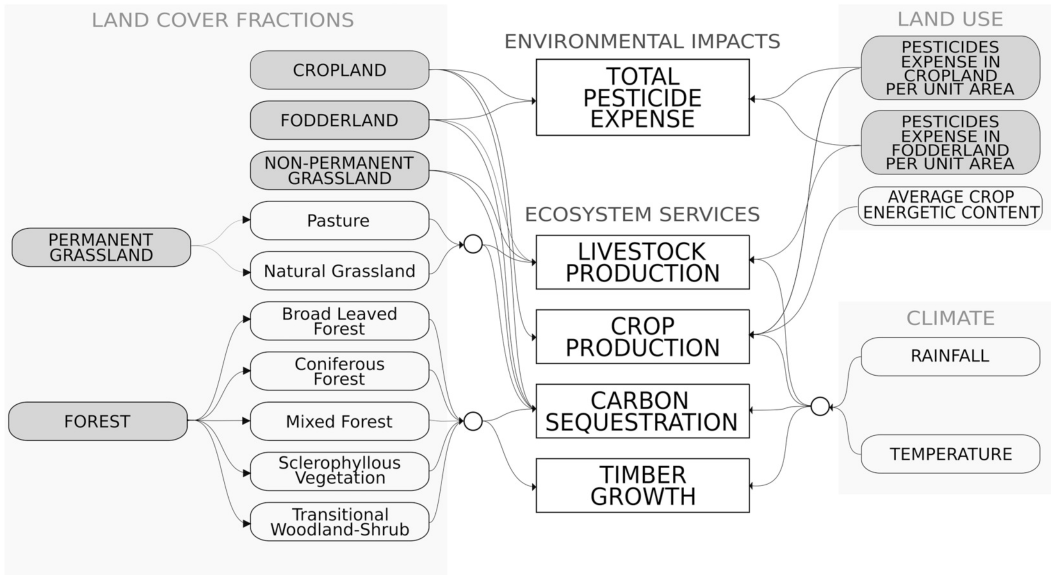

Fig. 1. Interactions between model inputs (rounded rectangles) and outputs (non-rounded rectangles). The inputs can be decision variables (grey rounded rectangles), intermediary variables (rounded rectangles with an arrow coming in), or production factors kept constant during the optimization procedure (rounded rectangles without an arrow coming in). The strength of the relationship was tested with the calibration procedure.

explored the possible sign combinations of the changes in livestock production and crop production and those of the changes in carbon sequestration and timber growth. If $\Delta f \leq 0$ and $\Delta e \leq 0$, none of the ecosystem services in the SAR increased.

2.2.2. *Analysis of the drivers of ecosystem services in the different groups of SARs*

For each group g found in the classification, we calculated the variation in ecosystem services per unit of management area $\Delta w_{s,\ g}$, the normalised changes in ecosystem service $\widetilde{\Delta w}_{s,g}$ (with formulas,

Table 2
Parameters (coefficients and exponents) of the Cobb-Douglas function used as a ecological production function for estimating the ecosystem services provision (crop production, livestock production, carbon sequestration, and timber growth; see Eq. (5)) in a generic SAR. The coefficient α vary with ecosystem service and land cover. The exponents γ vary with ecosystem service, land cover, and production factors. The symbol "–" indicates that the production factor has no influence in the provision of a given ecosystem service for given land use and production factor. The production factors are p_{FOD} and p_C, representing the pesticide expense per unit area in fodderland (*FOD*) or cropland (*C*) [€ ha^{-1} yr^{-1}]; *k*, representing the average energetic content of cultivated crops; *R*, representing the mean annual rainfall [mm yr^{-1}], and *T*, representing mean annual temperature [°C].

Cobb-Douglas function parameters		α	Exponents γ				
Production factors		–	p_C	p_{FOD}	k	R	T
Crop production [Mcal yr^{-1}] $R^2 = 0.987$							
Cropland		7.910	0.284	–	1.339	0.243	0.348
Livestock production [Mcal yr^{-1}] $R^2 = 0.889$							
Fodderland		188.293	–	0.381	–	0.342	0
Non-permanent grassland		2.891	–	–	–	0.709	0
Permanent grassland[a]	(1)	1.022	–	–	–	0.701	0
	(2)	1.294	–	–	–	0.545	0
Carbon Sequestration [10^9 gC yr^{-1}] $R^2 = 0.819$							
Cropland		0.059[c]	–	–	–	0	0
Fodderland		0.051[c]	–	–	–	0.001	0.001
Non-permanent grassland		1.131[c]	–	–	–	0	0.450
Permanent grassland[a]	(1)	1.933[c]	–	–	–	0.002	0.453
	(2)	1.724[c]	–	–	–	0.001	0.454
Forest[b]	(1)	4.015[c]	–	–	–	0.004	0.460
	(2)	2.884[c]	–	–	–	0.004	0.480
	(3)	2.661[c]	–	–	–	0.002	0.454
	(4)	2.591[c]	–	–	–	0.001	0.262
	(5)	2.659[c]	–	–	–	0.001	0.076
Timber growth [m^3 yr^{-1}] $R^2 = 0.870$							
Forest[b]	(1)	0.501[c]	–	–	–	0.321	0
	(2)	0.103[c]	–	–	–	0.493	0.387

[a] Divided into sub-fractions: (1) *Pastures* (CLC 231); (2) *Natural Grasslands* (CLC 321).
[b] Divided into sub-fractions: (1) *Broad Leaved Forests* (CLC 311); (2) *Coniferous Forest* (CLC 312); (3) *Mixed Forest* (CLC 313); (4) *Sclerophyllous Vegetation* (CLC 323); (5) *Transitional Woodland-Shrub* (CLC 324).
[c] To be multiplied by 10^4.

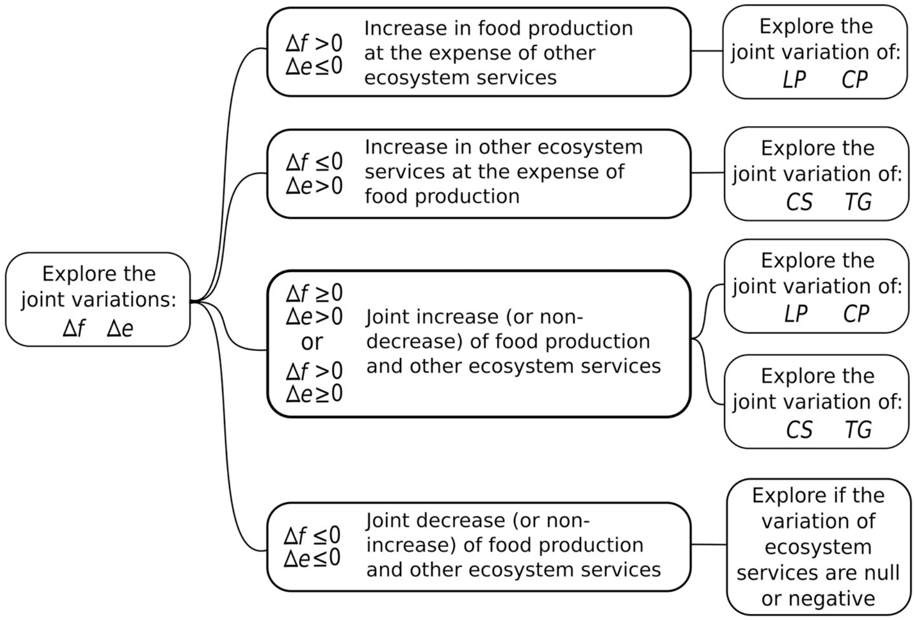

Fig. 2. Decision tree for the analysis of the variation in ecosystem services. Δf represents the maximum between the normalised livestock production (LP) and the normalised crop production (CP). Δe represents the maximum between the normalised carbon sequestration (CS) and the normalised timber growth (TG).

analogous to Eq. (7) and Eq. (8), reported in Table 1), the change in land use fractions $\Delta\theta_{l,\ g}$, and the change in pesticide expense in fodderland $\Delta w_{PE,\ FOD,\ g}$ and cropland $\Delta w_{PE,\ C,\ g}$ (formulaic expressions are given in Table 1).

3. Results

The evolutionary algorithm modified the land covers and land uses in the SARs, improving livestock production by 20% on a national scale while ensuring no loss of other ecosystem services and no increase in total pesticide expense. Thus, the trade-offs between ecosystem services could be softened to a certain extent. The ecosystem services other than livestock production did not increase at the national level. The classification of the SARs based on changes in food production and other ecosystem services identified five groups of SARs exhibiting distinct patterns of change in the amounts of ecosystem services provided, which were due to the changes in land cover and land use invoked by the optimization procedure.

3.1. Exploring the joint changes in ecosystem services

The five groups of SARs identified by the decision tree analysis of Δf and Δe are shown in Fig. 3. In Group 1, comprising 48% of the SARs, food production increased and the other ecosystem services decreased (or did not change) ($\Delta f > 0$, $\Delta e \le 0$). In Group 2, comprising 24% of the SARs, food production decreased (or did not change) and the other ecosystem services increased ($\Delta f \le 0$, $\Delta e > 0$). In Group 3, comprising 16% of the SARs, both food production and the other ecosystem services increased ($\Delta f > 0$, $\Delta e > 0$). In Group 4, comprising 4% of the SARs, at least one of the ecostystem service decreased and the other ecosystem remained constant, such that no ecosystem service increased. In Group 5, comprising 8% of the SARs, there was no change in any of the ecosystem services. Increases in ecosystem services in Groups 1, 2, and 3 compensated for the losses of ecosystem services in Group 4. In Group 5, changes in land cover and land use were not possible due to the constraints posed. We explored the joint changes in the ecosystem services in Groups 1, 2, and 3 further (Fig. 4).

In the SARs of Group 1, the changes in carbon sequestration and timber growth were negative, so we explored the joint changes in livestock production and crop production. The SARs of Group 1 fell into

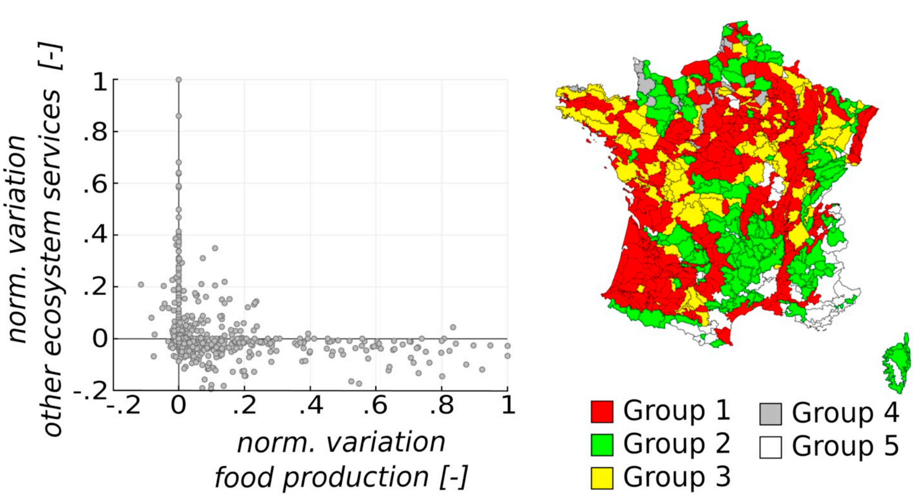

Fig. 3. Joint changes in aggregated indices of ecosystem services in different SARs. The indices represent food production and other ecosystem services. The different groups of SARs based on the changes in ecosystem services are identified on the map: Group 1, increase in food production and decrease (or no change) in other ecosystem services; Group 2, decrease (or no change) in food production and decrease in other ecosystem services; Group 3, increase in both food production and other ecosystem services; Group 4, decrease or no change in all ecosystem services (at least one ecosystem services decreases); Group 5, no changes in any ecosystem services.

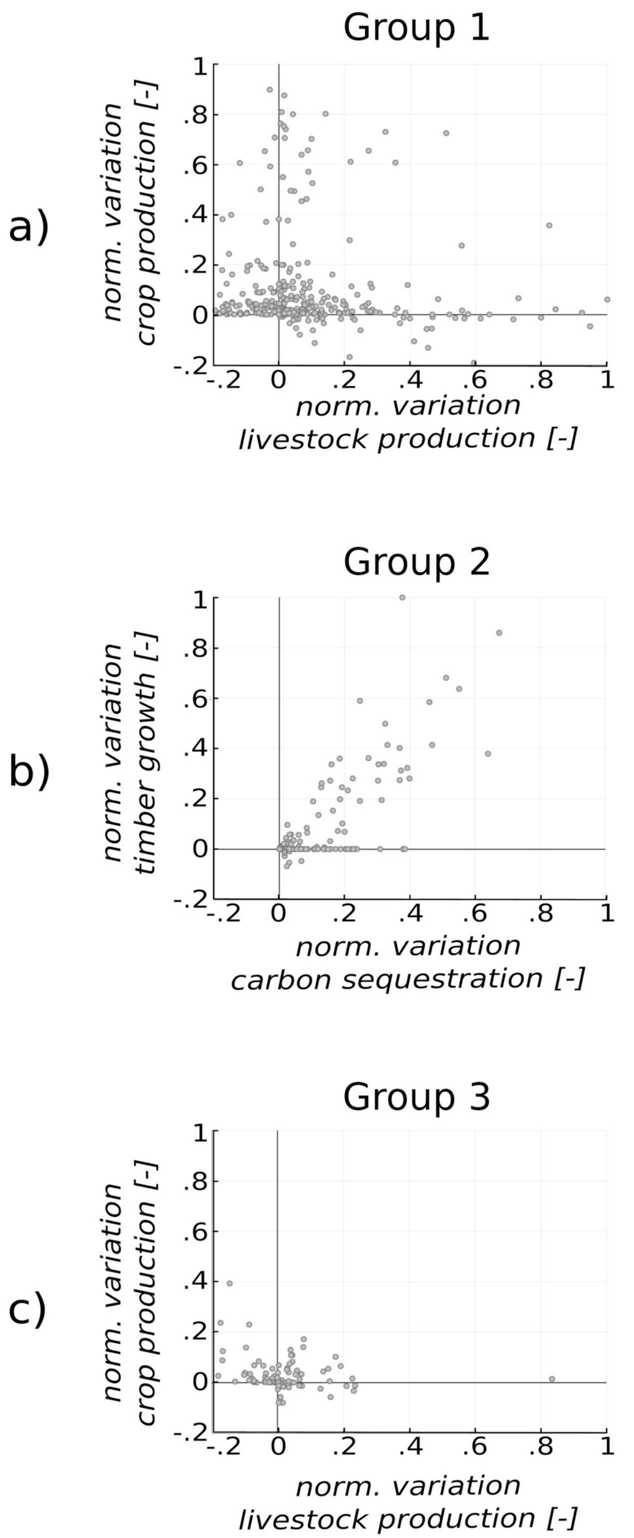

Fig. 4. Joint changes in the ecosystem services in Groups 1, 2, and 3 identified in the first step of the decision tree (depicted in Fig. 3). Panel (a) represents jointly the normalised changes in livestock production and crop production (being the changes in carbon sequestration and timber growth both negative). Panel (b) represents jointly the normalised changes in carbon sequestration and timber growth (being the changes in livestock production and crop production both negative). Panel (c) represents jointly the normalised changes in livestock production and crop production (being the changes in timber growth negative and carbon sequestration positive).

three sub-groups (Fig. 4a): those in which livestock production increased and crop production decreased ($\Delta w_{LP,g} > 0$, $\Delta w_{CP,g} \leq 0$, Group 1.1), those in which livestock production decreased and crop production increased ($\Delta w_{LP,g} \leq 0$, $\Delta w_{CP,g} > 0$, Group 1.2), and those in which both livestock production and crop production increased ($\Delta w_{LP,g} > 0$, $\Delta w_{CP,g} > 0$, Group 1.3).

In the SARs of Group 2, the changes in livestock production and crop production were negative, so we explored the joint changes in carbon sequestration and timber growth. The SARs of Group 2 fell into two groups (Fig. 4b): those in which both carbon sequestration and timber growth increased ($\Delta w_{CS,g} > 0$, $\Delta w_{TG,g} > 0$, Group 2.1) and those in which carbon sequestration increased and timber growth decreased ($\Delta w_{CS,g} > 0$, $\Delta w_{TG,g} \leq 0$, Group 2.2). We did not find SARs in which timber growth increased and carbon sequestration decreased.

In the SARs of Group 3, the changes in both food production and the other ecosystem services were positive, while we verified that carbon sequestration always increased and timber growth always decreased (results not shown). We explored the joint changes in livestock production and crop production. The SARs of Group 3 fell into three sub-groups, each characterised by an increase in carbon sequestration and a decrease in timber growth (Fig. 4c): those in which livestock production increased and crop production decreased (or did not change) ($\Delta w_{LP,g} > 0$, $\Delta w_{CP,g} \leq 0$, $\Delta w_{CS,g} > 0$, $\Delta w_{TG,g} < 0$, Group 3.1), those in which livestock production decreased (or did not change) and crop production increased ($\Delta w_{LP,g} \leq 0$, $\Delta w_{CP,g} > 0$ $\Delta w_{CS,g} > 0$, $\Delta w_{TG,g} < 0$, Group 3.2), and those in which both livestock production and crop production increased ($\Delta w_{LP,g} > 0$, $\Delta w_{CP,g} > 0$ $\Delta w_{CS,g} > 0$, $\Delta w_{TG,g} < 0$, Group 3.3).

3.2. Analysis of the drivers

We analysed (Fig. 5) the changes in the decision variables in the groups characterised by at least one positive change in one ecosystem service (i.e. Groups 1.1, 1.2, 1.3, 2.1, 2.2, 3.1, 3.2, 3.3).

The changes in land covers and pesticide expense within each group (Fig. 5) revealed how the drivers changed the ecosystem services, resulting in trade-offs or synergies. In Group 1.1, livestock production increased because of expansion and intensification of fodderland, which came at the expense of all the other land covers, causing a decrease in all of the other ecosystem services. In Group 1.2, crop production increased because of expansion and intensification of cropland, which came at the expense of fodderland, non-permanent grassland, and forest, while there was a small expansion of permanent grassland. In Group 1.3, livestock and crop production increased because of expansion and intensification of fodderland and cropland, which provoked a large reduction in non-permanent grassland and forest, resulting in decreased carbon sequestration and timber growth; as in Group 1.2, there was a slight expansion of permanent grassland. In Group 2.1, carbon sequestration and timber growth increased because of forest expansion (a common driver of those two ecosystem services). That group had little cropland and fodderland, so the expansion of forest came mostly at the expense of non-permanent and permanent grasslands. In Group 2.2, carbon sequestration increased because of expansion of permanent grassland at the expense of a slight part of forest, cropland, and fodderland, which decreased the other ecosystem services. In Group 3.1, livestock production and carbon sequestration increased because of expansions of fodderland and permanent grassland. The fodderland was intensified, and permanent grassland was a common driver of the two increased ecosystem services. In Group 3.2, crop production and carbon sequestration increased because of a slight expansion and intensification of cropland and a large expansion of permanent grassland. The other land covers were reduced, causing decreases of the remaining ecosystem services. Group 3.3 was the only group in which three ecosystem services increased (livestock production, crop production, and carbon sequestration). In that group, permanent grassland was highly expanded, mostly at the expense of non-

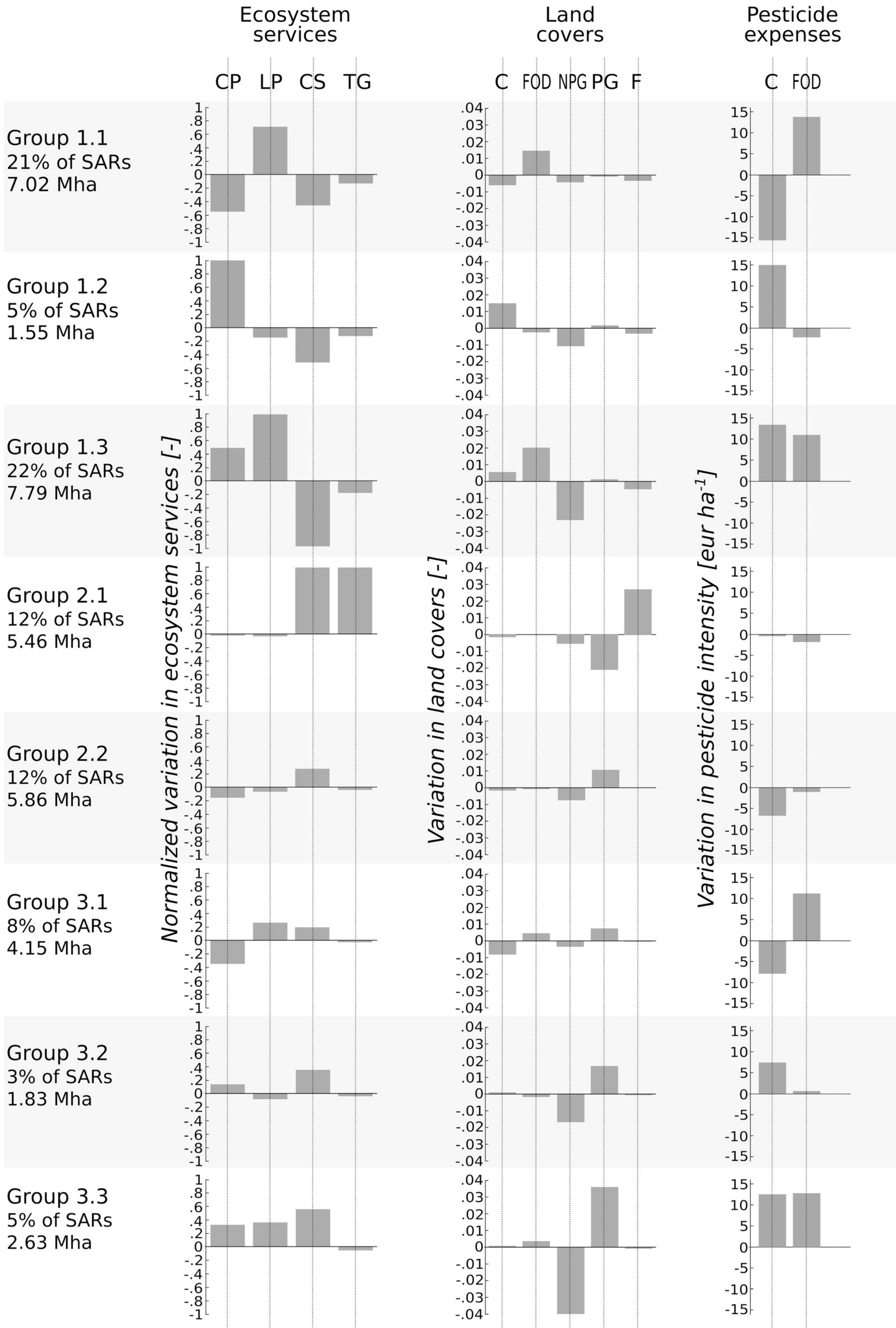

Fig. 5. Statistics of the results obtained for each group g (represented in each row), groups 4 and 5 are not included. The first column gives the percentage of SARs and total management area composing the group. The second column gives the normalised changes in ecosystem services per unit area ($\widetilde{\Delta w_{s,g}}$ as defined in Table 1), i.e., livestock production (*LP*), crop production (*CP*), carbon sequestration (*CS*), and timber growth (*TG*). The third column gives the change in land cover ($\Delta\theta_{l,\ g}$ as defined in Table 1), i.e. fodderland (*FOD*), cropland (*C*), non-permanent grassland (*NPG*), permanent grassland (*PG*), and forest (*F*) as a fraction of total management area of the group. The fourth column gives the change in pesticide expense per unit area ($\Delta t_{PE,\ l,\ g}$ as defined in Table 1) of cropland (*C*) or fodderland (*FOD*).

permanent grassland. Cropland and fodderland expanded only slightly but were much intensified.

4. Discussion

We modelled the provision of ecosystem services to investigate how land cover and land use could be allocated in farming systems (identified as the SARs) so to enhance the synergies and soften the trade-offs between livestock production and other ecosystem services. The results showed that a 20% increase in livestock production nationally could be achieved while maintaining other ecosystem services and without increasing total pesticide expense. That overall result included spatial variation across the country, meaning that for achieving a target at the national level, different land cover and land use allocations are required across SARs.

We found three groups of SARs within which at least one ecosystem service increased (Groups 1, 2, and 3), one small group of SARs where no ecosystem service increased and at least one decreased (Group 4) and one group of SARs where ecosystem services had no variation (Group 5). We deepened the analysis in groups 1, 2, and 3 (arriving to a further sub-division into a total of 8 groups). In Groups 4 and 5 the constraints were too restrictive that the optimization procedure could not increase pesticide expense or land cover fractions. The variation in the levels of ecosystem services revealed that not all ecosystem services could be increased within the same SAR. Driver analysis showed that some land covers were able to promote livestock production and other ecosystem services at the same time. Those results provided a quantitative picture of the trade-offs and synergies between ecosystem services that are linked to livestock production. By analysing the changes in the decision variables, we could infer contrasting land management strategies to soften the trade-offs and promote the synergies between livestock production and other ecosystem services.

4.1. Softening trade-offs

Trade-offs emerged because of limited land availability (Anderson-Teixeira et al., 2012; Metzger et al., 2006) and the constraints on pesticide expense. Some land covers (i.e. cropland and forest) were good for some ecosystem services but not for livestock production (see Fig. 1 and Table 2). That implies that the allocation of one land cover promotes one ecosystem service at the expense of another ecosystem service. Our results suggested two land management strategies for softening such trade-offs: intensification and spatial segregation of functions.

4.1.1. Intensification

A strategy to increase food production while leaving space for other ecosystem services is to decrease and intensify the space dedicated to agriculture (Phalan et al., 2010). In some of the SARs in our analysis (Groups 3.1 and 3.3), grasslands was expanded while cropland or fodderland were reduced and intensified, promoting both food production and carbon sequestration. That strategy corresponds to land sparing (Green et al., 2005), as a more food-productive land cover was reduced and intensified to allow for the expansion of grassland, which provided other ecosystem services.

4.1.2. Spatial segregation of functions

With the constraints imposed at the national level, it was possible to achieve some local loss of ecosystem services while compensating for those losses with gains in the same ecosystem services in other parts of the country (see Seppelt et al., 2013). That resulted in the intensification and arable expansion within some SARs (Group 1) and grassland and forest expansion within other SARs (Group 2). For a few SARs, there was a decrease in all ecosystem services. The spatial segregation of function allowed livestock production to be increased without losing other ecosystem services at the national level. Segregation has been a cost-effective way to increase both agricultural revenue and carbon sequestration in modelling experiments on Eastern Europe (Ruijs et al., 2013). The spatial segregation between food production and other ecosystem services corresponds to a land sparing strategy at the national level, which has already been reported as a way to reconcile food production and biodiversity conservation (Teillard et al., 2016).

Such spatial segregation could be seen as a displacement phenomenon (Meyfroidt and Lambin, 2009). Our results included a displacement phenomenon across regions within the same country: the improvement of environmental conditions in one region (e.g. the expansion of forest and grassland) was accompanied by the degradation of environmental conditions in another region. In our optimization model, the expansion of agriculture was constrained such that it occurred in SARs where a small amount of deforestation was possible. The constraint was in agreement with a principle of commodity crop expansion (Meyfroidt et al., 2014), which states that the accessibility of land determines agricultural expansion. Although it softened the trade-offs between livestock production and other ecosystem services, the spatial segregation of functions was not necessarily a positive outcome for all of the SARs, as SARs with higher intensification could support severe environmental pollution, which would have detrimental effects on biodiversity (Benton et al., 2003; Teillard et al., 2016). Thus, spatial segregation could lead to environmental inequalities (Larrère, 2017) between people living in regions with severe environmental degradation (due to the expansion and intensification of agriculture) and people living in regions with better environmental quality (due to the expansion of grassland and forest).

4.2. Promotion of land covers providing multiple services

The increase of livestock production and carbon sequestration in the same SARs was associated with the expansion of permanent grassland. The results of the calibration procedure showed that both non-permanent grassland and permanent grassland increased livestock production and carbon sequestration, however permanent grassland was more efficient in carbon sequestration, thus more adapted for promoting the synergy between livestock production and carbon sequestration. The multifunctionality of permanent grassland (Hector et al., 1999; Soussana and Lemaire, 2014) was evident in Group 3.1 and Group 3.3 (in total the 13% of the SARs), where both livestock production and carbon sequestration increased, and in Groups 1.2, 1.3, and 2.2 and 3.2 (together constituting 42% of the SARs), even if the expansion of permanent grassland was not sufficient to provoke a local increase in livestock production. In Group 3.3 (5% of the SARs), the massive expansion of grassland did contribute to increased livestock production. Our results provide quantitative evidence supporting the results of other studies in which the expansion of grassland, rather than that of other land covers, benefited ecosystem services and biodiversity (Freibauer et al., 2004; Soussana and Lemaire, 2014; Princé et al., 2015). The expansion of grassland was an efficient strategy also because grassland does not require the use of pesticides and makes it possible to increase livestock production by respecting the constraints of non-increase in pesticide expense.

Past studies have highlighted the risks of overly intensified grassland: overstocking could cause excessive greenhouse gas emissions and ammonia production that would counterbalance the positive effect on carbon sequestration (Bouwman et al., 1997; Dobbie and Smith, 2003). Recent studies demonstrated that accurate management of grasslands (Soussana and Lemaire, 2014; Loucougaray et al., 2015) based on the fine-tuning of livestock densities can enhance the synergy between carbon sequestration and livestock production. Similar management options have been proposed to enhance the synergy between livestock grazing and biodiversity in grasslands (Tichit et al., 2005a, 2005b; Ravetto Enri et al., 2017). Our results provide further evidence of the multifunctionality of grassland by showing quantitatively how grassland promotes synergy between livestock production and other ecosystem services. The expansion of grassland for the provision of multiple ecosystem services can be seen as a land sharing strategy (Green et al., 2005).

The expansion of grassland, which is better than fodderland for carbon sequestration but inferior to fodderland for livestock production, was associated with an intensification of a reduced fodderland area. That relationship was visible in Groups 3.1 and 3.3, where the expansion of grassland and intensification of fodderland produced local net increases in carbon sequestration and livestock production, and also in Groups 1.1, 1.3, where fodderland was intensified. Those results are analogous to the results obtained by Lamb et al. (2016), who showed that forest expansion to mitigate the greenhouse gas emitted by agriculture in the U.K. required the intensification of arable land, which caused other environmental impacts.

Our results highlight the advantages of land covers that provide multiple ecosystem services. Forest provided carbon sequestration and timber growth, a synergy that indirectly involved livestock production by saving space that could be used to soften the trade-off between livestock production and other ecosystem services. Other studies showed that cropland can also be multifunctional by providing food for humans and feed for livestock, notably through the use of by-products (Van Zanten et al., 2016; Mottet et al., 2017). A high level of multifunctionality is also reported in mixed systems where crop production and livestock production are integrated (Herrero et al., 2010; Bonaudo et al., 2014; Dumont et al., 2013).

4.3. Livestock and the land sparing–sharing debate

The relationship between livestock production and other ecosystem services feeds into the debate on land sparing–sharing (Green et al., 2005; Phalan et al., 2011). In line with the recommendation of Kremen (2015), we extended the land sparing–sharing debate to multiple ecosystem services. We found that livestock production goes beyond the land sharing–sparing dichotomy. Its close linkage to grassland and fodderland generated a hybrid solution, which is illustrated in the SARs where fodderland was reduced and intensified (land sparing) in order to reap the benefits of grassland expansion (land sharing). Finally, our findings supported multi-scale land sparing (Fischer et al., 2014), with a reduction and intensification of cultivated land at the local level and a spatial segregation of food production and other ecosystem services at the national level.

4.4. Approach limitations and perspectives

The model we developed is strongly based on data, therefore it is valid only in the range of data used for calibration of the parameters and it can be applied only if data are available all over the target study area. We considered only the production factors and the decision variables related to our research questions, therefore the results are driven by the choice of these variables. However we believe this is a first step to highlight some mechanisms related to strategies for softening trade-offs and enhancing synergies between livestock production and other ecosystem services. In the way it is formulated, the model can be easily extended. The Cobb-Douglas function has been already selected in other studies (e.g., Onofri et al., 2017) for its goodness of fit with data and simplicity at the same time. Upon data availability, other production factors can be easily included in the function, for example fertilizer input or more economic variables such as labour intensity. The modelling approach can be easily adapted to answering other research question. For example, the crop composition and association can be used as a lever to soften ecosystem services trade-offs. Last but not least, other optimization scenarios can be formulated for answering new research questions, for example other ecosystem services (e.g., carbon sequestration) could be maximised posing constraints on the remaining.

5. Conclusions

Our results highlight trade-offs and synergies between livestock production and other ecosystem services. The main strategy to cope with the trade-offs involved land sparing at both the local and the national levels. The main strategy to enhance the synergies was based on the expansion of grasslands in order to benefit from the multifunctionality of that land cover type in terms of livestock production and carbon sequestration. We identified a large number of SARs (55% of the total) where grassland was expanded. In a small number of SARs (13% of the total), we identified a local net increase in both livestock production and carbon sequestration. Future policies to improve the provision of multiple ecosystem services should seek to expand multifunctional areas.

Acknowledgments

The authors are thankful to Sophie Martin and two anonymous reviewers who helped to improve the quality of the manuscript. FA was supported by a grant overseen by the French National Research Agency (ANR) as part of the "Investment d'Avenir" Programme (LabEx BASC; ANR-11-LABX-0034) (project API-SMAL). CD was supported by the European Commission within the Seventh Framework Programme in the frame RURAGRI ERA-NET under Grant Agreement no. 235175 TRUSTEE (ANR-13-RURA-0001-01). MT was supported by the European Union's Horizon 2020 Research & Innovation Programme under grant agreement no 696231 [SusAn] (project ANIMALFUTURE). Neither the API-SMAL project, The TRUSTEE project, the ANIMALFUTURE project, nor any of their partner organizations, any organization of the European Union, or European Commission is accountable for the content of this research. The funders had no role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Appendix 1. Scenario constraints

The constraints posed in the different SARs took into account the land suitability to crop or livestock and how that suitability varies across France. We based the land suitability on livestock type regions (Perrot et al., 2013; Fig. A1), each of which had specific constraints (Table A1).

We calibrated the parameters in the ranges given by the French data. Therefore, during the optimization processes, we imposed constraints to prevent the values of the decision variables from going out of those ranges. In each livestock region, we imposed for each variable a minimum value m and a maximum value M. At the initialisation of the optimization procedure, if the value of a variable in a SAR was below m, that value could not decrease. Analogously, if the value was above M, it could not increase. If the value was between m and M, it could increase or decrease within the range $[m; M]$. In general, we made m and M equal to q^- and q^+ (the 0.25 and 0.75 quantiles calculated from the French data for all of the SARs of the livestock type area), respectively. Those constraints prevented the values of the decision variables from going out of the range given by the French data. In some cases, we included other, more restrictive, policy or biophysical constraints. We defined constraints to prevent the reduction of forest, except in highly productive areas (regions 0, 1, 1.1, 2, and 2.1) where a small decrease (down to 95% or more of the starting value) in permanent grassland and forest would enable the expansion of more intensive land covers. Forest expansion was not feasible in those highly productive areas. In region 3, we did not allow permanent grassland or forest to decrease, nor did we allow cropland or fodderland to increase. In regions 4 and 4.1, we allowed slight increases (of up to 105% of the starting value) in cropland, fodderland, and the pesticide expenses for those land covers. Furthermore, in regions 4 and 4.1, we allowed the transformation of non-permanent grassland into permanent grassland. In regions 5 and 5.1, we allowed no changes in cropland, fodderland, and the pesticide expenses for those two land covers. We allowed forest to be increased to up to 110% of the starting value in regions 5 and 5.1 and up to two-thirds of the management area in region 7. In regions 6 and 6.1, we allowed decreases in cropland and fodderland, and we allowed forest expansion to up to two-thirds of the management area.

Table A1
Ranges of variation in the land cover fractions (cropland *C*, fodderland *FOD*, non-permanent grassland *NPG*, permanent grassland *PG*, and forest *F*) and pesticide expense for cropland p_C and fodderland p_{FOD} allowed in the SARs of the different livestock type regions during the Optimization process. The initial variables in the SARs are indicated by $\overline{C}$, $\overline{FOD}$, $\overline{NPG}$, $\overline{PG}$, $\overline{F}$, $\overline{p_C}$, and $\overline{p_{FOD}}$.

Region	C	FOD	NPG	PG	F	$P_{C,0}$	$p_{FOD,0}$
0	$[q^-; q^+]$	$[q^-; q^+]$	$[q^-; q^+]$	$[0.95\overline{PG}; q^+]$	$[0.95\overline{F}; \overline{F}]$	$[q^-; q^+]$	$[q^-; q^+]$
1	$[q^-; q^+]$	$[q^-; q^+]$	$[q^-; q^+]$	$[0.95\overline{PG}; q^+]$	$[0.95\overline{F}; \overline{F}]$	$[q^-; q^+]$	$[q^-; q^+]$
1.1	$[q^-; q^+]$	$[q^-; q^+]$	$[q^-; q^+]$	$[0.95\overline{PG}; q^+]$	$[0.95\overline{F}; \overline{F}]$	$[q^-; q^+]$	$[q^-; q^+]$
2	$[q^-; q^+]$	$[q^-; q^+]$	$[0.5\,\overline{NPG}; q^+]$	$[0.95\overline{PG}; q^+]$	$[0.95\overline{F}; \overline{F}]$	$[q^-; q^+]$	$[q^-; q^+]$
2.1	$[q^-; q^+]$	$[q^-; q^+]$	$[0.2\,\overline{NPG} q^+]$	$[0.95\overline{PG}; q^+]$	$[0.95\overline{F}; \overline{F}]$	$[q^-; q^+]$	$[q^-; q^+]$
3	$[q^-; \overline{C}]$	$[q^-; \overline{FOD}]$	$[q^-; q^+]$	$[\overline{PG}; q^+]$	–	$[q^-; \overline{p_C}]$	$[q^-; \overline{p_{FOD}}]$
4	$[q^-; 1.05\overline{C}]$	$[q^-; 1.05\overline{FOD}]$	$[q^-; q^+]$*	$[\overline{PG}; q^+]$	–	$[q^-; 1.05\overline{p_C}]$	$[q^-; 1.05\overline{p_{FOD}}]$
4.1	$[q^-; 1.05\overline{C}]$	$[q^-; 1.05\overline{FOD}]$	$[q^-; q^+]$*	$[\overline{PG}; q^+]$	–	$[q^-; 1.05\overline{p_C}]$	$[q^-; 1.05\overline{p_{FOD}}]$
5	–	–	$[q^-; \overline{NPG}]$*	$[q^-; q^+]$**	$[\overline{F}; 1.10\overline{F}]$	$[q^-; \overline{p_C}]$	$[q^-; \overline{p_{FOD}}]$
5.1	–	–	$[q^-; \overline{NPG}]$*	$[q^-; q^+]$**	$[\overline{F}; 1.10\overline{F}]$	$[q^-; \overline{p_C}]$	$[q^-; \overline{p_{FOD}}]$
6	$[q^-; \overline{C}]$	$[q^-; \overline{FOD}]$	$[q^-; q^+]$*	$[q^-; q^+]$**	$[\overline{F}; 0.67]$	$[q^-; \overline{p_C}]$	$[q^-; \overline{p_{FOD}}]$
6.1	$[q^-; \overline{C}]$	$[q^-; \overline{FOD}]$	$[q^-; q^+]$*	$[q^-; q^+]$**	$[\overline{F};0.67]$	$[q^-; \overline{p_C}]$	$[q^-; \overline{p_{FOD}}]$
7	–	–	$[q^-; \overline{NPG}]$*	$[q^-; q^+]$**	$[\overline{F}; 0.67]$	$[q^-; \overline{p_C}]$	$[q^-; \overline{p_{FOD}}]$

q^- represents the 0.25 quantile of the variable measured within all the SARs belonging to the livestock type region.
q^+ represents the 0.75 quantile of the variable measured within all the SARs belonging to the livestock type region.
− indicates that the variable cannot change.
* Indicates that the land cover type can only be transformed into permanent grassland.
** Indicates that the land cover type can only be transformed into forest.

Table A2
Ranges of variation of the different areas and pesticide expenses in the different livestock typology region. The ranges are expressed as [−x; +y] where x and y are percentages of the initial total areas (of cropland, fodderland, non-permanent grassland, permanent grassland, and forest) in each livestock typology region and percentage of the total pesticide expense in cropland and fodderland. The minimum (maximum) total pesticide expense allowed was obtained by multiplying the minimum (maximum) cropland or fodderland area allowed by the minimum (maximum) pesticide expense allowed in cropland or fodderland.

Region	Percentage of SARs	Cropland	Fodderland	Non Permanent Grassland	Permanent Grassland	Forest	Pesticide expense in cropland	Pesticide expense in fodderland
	[%]	Range of variation	Range of variation	Range of variation	Range of variation	Range of variation	Range of variation	Range of variation
0	24.5	[−37; +29]	[−85; +62]	[−79; +80]	[−5; +67]	[−5; +0]	[−54; +44]	[−93; +105]
1	15.7	[−34; +27]	[−69; 41%]	[−61; 85]	[−5; +51]	[−5; +0]	[−50; +38]	[−79; +82]
1.1	10.0	[−27; +57]	[−58; +76]	[−78; 34]	[−5; +55]	[−5; +0]	[−31; +117]	[−72; +112]
2	6.6	[−76; +92]	[−82; +5]	[−80; +10]	[−5; +135]	[−5; +0]	[−79; +120]	[−83; +20]
2.1	5.6	[−32; +646]	[−33; +355]	[−80; +81]	[−5; +10]	[−5; +0]	[−46; +757]	[−38; +441]
3	4.2	[−44; +0]	[−47: +0]	[−78: +47]	[−0; +40]	[−0; +0]	[−50; +0]	[−50; +0]
4	5.4	[−64; +5]	[−67; +5]	[−1; +227]	[−0; 50]	[−0; +0]	[−69; +10]	[−79; +10]
4.1	5.4	[−48; +5]	[−40; +5]	[−32: +22]	[−0; +14]	[−0; +0]	[−56; +10]	[−66; +10]
5	3.1	[−0; +0]	[−0; +0]	[−35; +0]	[−59; +26]	[−0; +10]	[−30; +0]	[−50; +0]
5.1	5.9	[−0; +0]	[−0; +0]	[−44; +0]	[−51; +74]	[−0; +10]	[−27; +0]	[−15; +0]
6	2.3	[−79; +0]	[−71; +0]	[−58; +199]	[−32; +97]	[−0; +8]	[−81; +0]	[−78; +0]
6.1	6.2	[−81; +0]	[−84; +0]	[−79; +35]	[−50; +39]	[−0; +35]	[−86; +0]	[−89; +0]
7	5.5	[−0; +0]	[−0; +0]	[−93; +0]	[−24; +45]	[−0; +2]	[−8; +0]	[−25; +0]
Total	100	[−41: +39]	[−66; +29]	[−65; +43]	[−16; +46]	[−2; +5]	[−53; +54]	[−72;+48]

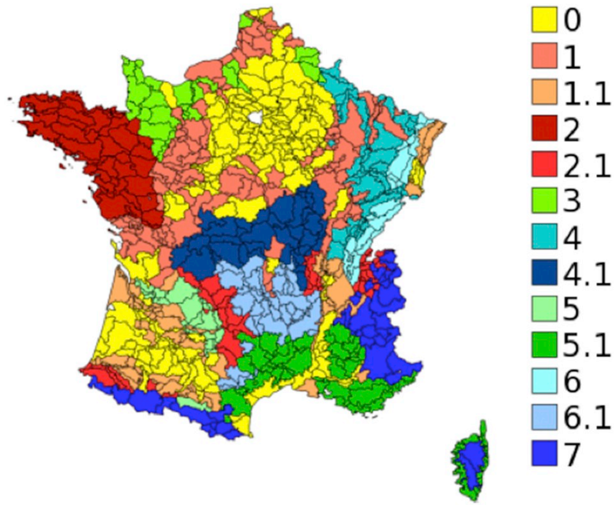

Fig. A1. Regions in France characterised by different livestock Systems according to Perrot et al. (2013). The livestock type regions and their corresponding identification codes were as follows: (0) Specialised crop areas with no livestock; (1) Mixed crop-livestock in the Parisian basin; (1.1) Mixed crop-livestock in the Aquitain basin, Rhône Alp, or Alsace, where livestock decreased more rapidly; (2) Western intensive livestock (dairy areas where there are no alternatives to livestock); (2.1) Intensive piedmont areas (beef production areas where there is little or no alternative to livestock); (3) North-western grassland-based areas; (4) North-eastern grassland-based areas (dairy tradition); (4.1) North Massif Central areas (beef tradition); (5) Causses (limestone plateaus) and southwest-hills pastoral areas; (5.1) Mediterranean pastoral areas; (6) Wet mountains of Franche-Comté and Vosges (with strong dairy specialisation); (6.1) Wet mountains of Auvergne and Massif Central (with mixed dairy-beef systems); (7) High mountains (Alps and Pyrenees)

References

Aleksandratos, N., Bruinsma, J., 2012. World agriculture towards 2030/2050. Land Use Policy 20, 375. https://doi.org/10.1016/S0264-8377(03)00047-4.

Anderson-Teixeira, K.J., Duval, B.D., Long, S.P., Delucia, E.H., 2012. Biofuels on the landscape: Is "land sharing" preferable to "land sparing"? Ecol. Appl. 22, 2035–2048. https://doi.org/10.1890/12-0711.1.

Barbier, E.B., 2007. Valuing ecosystem services as productive inputs. Econ. Policy 22, 178–229. https://doi.org/10.1111/j.1468-0327.2007.00174.x.

Bennett, E.M., Peterson, G.D., Gordon, L.J., 2009. Understanding relationships among multiple ecosystem services. Ecol. Lett. 12, 1–11. https://doi.org/10.1111/j.1461-0248.2009.01387.x.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: Is habitat heterogeneity the key? Trends Ecol. Evolution 18, 182–188. https://doi.org/10.1016/S0169-5347(03)00011-9.

Bonaudo, T., Burlamaqui, A., Sabatier, R., Ryschawy, J., Bellon, S., Magda, D., Tichit, M., 2014. Agroecological principles for the redesign of integrated crop – livestock systems. Eur. J. Agron. 57, 43–51. https://doi.org/10.1016/j.eja.2013.09.010.

Boumans, R., Costanza, R., Farley, J., Wilson, M.A., Portela, R., Rotmans, J., Villa, F.? Grasso, M., 2002. Modelling the dynamics of the integrated earth system and the value of global ecosystem services using the GUMBO model. Ecol. Econ. 41, 529–560. https://doi.org/10.1016/S0921-8009(02)00098-8.

Bouwman, A.F., Lee, D.S., Asman, W.A.H., Dentener, F.J., Van Der Hoek, K.W., Olivier, J.G.J., 1997. A global high-resolution emission inventory for ammonia. Glob. Biogeochem. Cycles 11, 561–587. https://doi.org/10.1029/97GB02266.

Butault, J.P., Dedryver, C.A., Gary, C., Guichard, L., Jacquet, F., Meynard, J.M., Nicot, P., Pitrat, M., Reau, R., Sauphanor, B., Savini, I., Volay, T., 2010. Ecophyto R&D. In: Quelle voies pour réduire l'usage des pesticides? Synthèse du rapport d'étude. INRA Editeur, France, pp. 90.

Butsic, V., Kuemmerle, T., 2015. Using optimization methods to align food production and biodiversity conservation beyond land sharing and land sparing. Ecol. Appl. 25, 589–595. https://doi.org/10.1890/14-1927.1.sm.

Chan, K.M.A., Shaw, M.R., Cameron, D.R., Underwood, E.C., Daily, G.C., 2006. Conservation planning for ecosystem services. PLoS Biol. 4, e379. https://doi.org/10.1371/journal.pbio.0040379.

De Jong, K., 2006. Evolutionary algorithms: a unified approach. MIT Press, Cambridge, MA.

Dobbie, K.E., Smith, K.A., 2003. Nitrous oxide emission factors for agricultural soils in Great Britain: The impact of soil water-filled pore space and other controlling variables. Glob. Chang. Biol. 9, 204–218. https://doi.org/10.1046/j.1365-2486.2003.00563.x.

Dross, C., Jiguet, F., Tichit, M., 2017. Concave trade-off curves between crop production and taxonomic, functional and phylogenetic diversity of birds. Ecol. Indic. 79, 83–90. https://doi.org/10.1016/j.ecolind.2017.03.046.

Dross, C., Princé, K., Jiguet, F., Tichit, M., 2018. Contrasting bird communities along production gradients of crops and livestock in French farmlands. Agric. Ecosyst. Environ. 253, 55–61. https://doi.org/10.1016/j.agee.2017.10.025.

Dumont, B., Fortun-Lamothe, L., Jouven, M., Thomas, M., Tichit, M., 2013. Prospects from agroecology and industrial ecology for animal production in the 21st century. Animal 7, 1028–1043. https://doi.org/10.1017/S1751731112002418.

Ericksen, P.J., Ingram, J.S.I., Liverman, D.M., 2009. Food security and global environmental change: emerging challenges. Environ. Sci. Pol. 12, 373–377. https://doi.org/10.1016/j.envsci.2009.04.007.

European Environmental Agency (EEA), 2013. CORINE Land Cover (CLC) 2006, Version 17. European Environmental Agency (EEA), Kopenhagen K, Denmark.

Fischer, J., Abson, D.J., Butsic, V., Chappell, M.J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H.G., von Wehrden, H., 2014. Land sparing versus land sharing: Moving forward. Conserv. Lett. 7, 149–157. https://doi.org/10.1111/conl.12084.

Foley, J.A., Defries, R.S., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Halloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Rammankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science 309, 570–574. https://doi.org/10.1126/science.1111772.

Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Mueller, N.D., O'Connell, C., Ray, D.K., West, P.C., Balzer, C., Bennett, E.M., Carpenter, S.R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., Tilman, D., Zaks, D.P.M., 2011. Solutions for a cultivated planet. Nature 478, 337–342. https://doi.org/10.1038/nature10452.

Freibauer, A., Rounsevell, M.D.A., Smith, P., Verhagen, J., 2004. Carbon sequestration in the agricultural soils of Europe. Geoderma 122, 1–23. https://doi.org/10.1016/j.geoderma.2004.01.021.

Gallaun, H., Zanchi, G., Nabuurs, G.J., Hengeveld, G., Schardt, M., Verkerk, P.J., 2010. EU-wide maps of growing stock and above-ground biomass in forests based on remote sensing and field measurements. For. Ecol. Manag. 260, 252–261. https://doi.org/10.1016/j.foreco.2009.10.011.

Giller, K.E., 2013. Guest editorial: can we define the term 'farming systems'? A question of scale. Outlook Agric. 42, 149–153. https://doi.org/10.5367/oa.2013.0139.

Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M., Toulmin, C., 2010. Food Security: The Challenge of Feeding 9 Billion People. Science 327, 812–818. https://doi.org/10.1126/science.1185383.

Green, R.E., Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M., Toulmin, C., Gallaun, H., Zanchi, G., Nabuurs, G.J., Hengeveld, G., Schardt, M., Verkerk, P.J., Freibauer, A., Rounsevell, M.D.A., Smith, P., Verhagen, J., Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Mueller, N.D., O'Connell, C., Ray, D.K., West, P.C., Balzer, C., Bennett, E.M., Carpenter, S.R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., Tilman, D., Zaks, D.P.M., DeFries, Foley R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkouski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., Fischer, J., Abson, D.J., Butsic, V., Chappell, M.J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H.G., von Wehrden, H., Dumont, B., Fortun-Lamothe, L., Jouven, M., Thomas, M., Tichit, M., Doxa, A., Bas, Y., Paracchini, M.L., Pointereau, P., Terres, J.M., Jiguet, F., Dobbie, K.E., Smith, K.A., Chan, K.M.A., Shaw, M.R., Cameron, D.R., Underwood, E.C., Daily, G.C., Butsic, V., Kuemmerle, T., Britschgi, A., Spaar, R., Arlettaz, R., Bouwman, A.F., Lee, D.S., Asman, W.A.H., Dentener, F.J., Van Der Hoek, K.W., Olivier, J.G.J., Bennett, E.M., Peterson, G.D., Gordon, L.J., Anderson-Teixeira, K.J., Duval, B.D., Long, S.P., Delucia, E.H., Alexandratos, N., Bruinsma, J., 2005. Farming and the Fate of Wild Nature. Science 307, 550–555. https://doi.org/10.1126/science.1106049.

Groot, J.C.J., Rossing, W.A.H., 2011. Model-aided learning for adaptive management of natural resources: an evolutionary design perspective. Methods Ecol. Evol. 2, 643–650. https://doi.org/10.1111/j.2041-210X.2011.00114.x.

Groot, J.C.J., Jellema, A., Rossing, W.A.H., 2010. Designing a hedgerow network in a multifunctional agricultural landscape: Balancing trade-offs among ecological quality, landscape character and implementation costs. Eur. J. Agron. 32, 112–119. https://doi.org/10.1016/j.eja.2009.07.002.

Groot, J.C.J., Oomen, G.J.M., Rossing, W.A.H., 2012. Multi-objective optimization and design of farming systems. Agric. Syst. 110, 63–77. https://doi.org/10.1016/j.agsy.2012.03.012.

Hallmann, C.A., Foppen, R.P.B., van Turnhout, C.A.M., de Kroon, H., Jongejans, E., 2014. Distribution and formation of Mima-like earth mounds in the western Cape Province of South Africa. Nature 511, 341–343. https://doi.org/10.1038/nature13531.

Hansen, N., Ostermeier, A., 2001. Completely derandomized self-adaptation in evolution strategies. Evol. Comput. 9, 159–195. https://doi.org/10.1162/106365601750190398.

Haylock, M.R., Hofstra, A.M.G., Klein Tank, A.M.G., Klok, E.J., Jones, P.D., New, M., 2008. A European daily high-resolution gridded data set of surface temperature and precipitation for 1950-2006. J. Geophys. Res.-Atmos. 113, D20119. https://doi.org/10.1029/2008JD010201.

Heck, V., Hoff, H., Wirsenius, S., Meyer, C., Kreft, H., 2018. Land use options for staying within the Planetary Boundaries - Synergies and trade-offs between global and local sustitutability goals. Global Environ. Chang. 49, 73–84. https://doi.org/10.1016/j.gloenvcha.2018.02.004.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Högberg, P., Huss-Dannell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.-D., Siamantziouras, A.-S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., Lawton, J.H., 1999. Plant Diversity and Productivity Experiments in European Grasslands. Science 286, 1123–1127. https://doi.org/10.1126/science.286.5442.1123.

Herrero, M., Thornton, P.K., 2013. Livestock and global change: Emerging issues for sustainable food systems. Proc. Natl. Acad. Sci. 110, 20878–20881. https://doi.org/10.1073/pnas.1321844111.

Herrero, M., Thornton, P.K., Notenbaert, A.M., Wood, S., Msangi, S., Freeman, H.A., Bossio, D., Dixon, J., Peters, M., van de Steeg, J., Lynam, J., Rao, P.P., MacMillan, S., Gerard, B., McDermott, J., Sere, C., Rosegrant, M., 2010. Smart Investments in Sustainable Food Production: Revisiting Mixed Crop-Livestock Systems. Science 327, 822–825. https://doi.org/10.1126/science.1183725.

Holman, L.P., Brown, C., Janes, V., Sandars, D., 2017. Can we be certain about future land use change in Europe? A multi-scenario, integrated-assessment analysis. Agric. Syst. 151, 126–135. https://doi.org/10.1016/j.agsy.2016.12.001.

Jopke, C., Kreyling, J., Maes, J., Koellner, T., 2014. Interactions among ecosystem services across Europe: Bagplots and cumulative correlation coef fi cients reveal synergies, trade-offs, and regional patterns. Ecol. Indic. 49, 46–52. https://doi.org/10.1016/j.ecolind.2014.09.037.

Kastner, T., Ibarrola Rivas, M.J., Koch, W., Nonhebel, S., 2012. Global changes in diets and the consequences for land requirements for food. Proc. Natl. Acad. Sci. 109, 6868–6872. https://doi.org/10.1073/pnas.1117054109.

Klatzmann, J., 1995. la localisation des cultures et des productions animales en France. Tech. rep. ed.

Kremen, C., 2015. Reframing the land-sparing/land-sharing debate for biodiversity conservation. Ann. N. Y. Acad. Sci. 1355, 52–76. https://doi.org/10.1111/nyas.12845.

Lamb, A., Green, R., Bateman, I., Broadmeadow, M., Bruce, T., Burney, J., Carey, P., Chadwick, D., Crane, E., Field, R., Goulding, K., Griffiths, H., Hastings, A., Kasoar, T., Kindred, D., Phalan, B., Pickett, J., Smith, P., Wall, E., Zu Ermgassen, E.K.H.J., Balmford, A., 2016. The potential for land sparing to offset greenhouse gas emissions from agriculture. Nat. Clim. Chang. 6, 488–492. https://doi.org/10.11138/nclimate2910.

Larrère, C., 2017. Le inégalités environmentales. Presse Universitaire de France, Paris, France.

Lemaire, G., Wilkins, R., Hodgson, J., 2005. Challenges for grassland science: Managing research priorities. Agric. Ecosyst. Environ. 108, 99–108. https://doi.org/10.1016/j.agee.2005.01.003.

Loucougaray, G., Dobremez, L., Gos, P., Pauthenet, Y., Nettier, B., Lavorel, S., 2015. Assessing the Effects of Grassland Management on Forage Production and Environmental Quality to Identify Paths to Ecological Intensification in Mountain Grasslands. Environ. Manag. 56, 1039–1052. https://doi.org/10.1007/s00267-015-0550-9.

Lovell, S.T., DeSantis, S., Nathan, C.A., Olson, M.B., Méndez, V.E., Kominami, H.C., Erickson, D.L., Morris, K.S., Morris, W.B., 2010. Integrating agroecology and landscape multifunctionality in Vermont: An evolving framework to evaluate the design of agroecosystems. Agric. Syst. 103, 327–341.

Maes, J., Paracchini, M.L., Zulian, G., 2011. A European assessment of the provision of ecosystem services. Towards an atlas of ecosystem services. JRC Scientific and Technical Reports. Publications Office of the European Union, Luxembourg.

Memmah, M.M., Lescourret, F., Yao, X., Lavigne, C., 2015. Metaheuristics for agricultural land use optimization. A review. Agron. Sustain. Dev. 35, 975–998. https://doi.org/10.1007/s13593-015-0303-4.

Metzger, M.J., Rounsevell, M.D.A., Acosta-Michlik, L., Leemans, R., Schröter, D., 2006. The vulnerability of ecosystem services to land use change. Agric. Ecosyst. Environ. 114, 69–85. https://doi.org/10.1016/j.agee.2005.11.025.

Meyfroidt, P., Lambin, E.F., 2009. Forest transition in Vietnam and displacement of deforestation abroad. Proc. Natl. Acad. Sci. 106, 16139–16144. https://doi.org/10.1073/pnas.0904942106.

Meyfroidt, P., Carlson, K.M., Fagan, M.E., Gutiérrez-Vélez, V.H., Macedo, M.N., Curran, L.M., Defries, R.S., Dyer, G.A., Gibbs, H.K., Lambin, E.F., Morton, D.C., Robiglio, V., 2014. Multiple pathways of commodity crop expansion in tropical forest landscapes. Environ. Res. Lett. 9, 74012. https://doi.org/10.1088/1748-9326/9/7/074012.

Millenium Ecosystem Assessment, 2005. Ecosystems and human well-being: biodiversity synthesis. World Resources Institute, Washington, DC, USA.

Monfreda, C., Ramankutty, N., Foley, J.A., 2008. Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. Global Biogeochem. Cycle 22, 1–19. https://doi.org/10.1029/2007GBB002947.

Morelli, F., Jiguet, F., Sabatier, R., Dross, C., Princé, K., Tryjanowski, P., Tichit, M., 2017. Spatial covariance between ecosystem services and biodiversity pattern at a national scale (France). Ecol. Indic. 82, 574–586. https://doi.org/10.1016/j.ecolind.2017.04.036.

Mottet, A., de Haan, C., Falcucci, A., Tempio, G., Opio, C., Gerber, P., 2017. Livestock: On our plates or eating at our table? A new analysis of the feed/food debate. Glob. Food Sec. 14, 1–8. https://doi.org/10.1016/j.gfs.2017.01.001.

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, 617–626. https://doi.org/10.1016/j.ecolecon.2010.12.006.

Onofri, L., Lange, G.M., Portela, R., Nunes, P.A.L.D., 2017. Valuing ecosystem services for improved national accounting: a pilot study from Madagascar. Ecosyst. Serv. 23, 116–126. https://doi.org/10.1016/j.ecoser.2016.11.016.

Perrot, C., Barbin, G., Bossis, N., Champion, F., Morhain, B., Morin, E., 2013. L'élevage d'herbivores au Recensement agricole 2010 - Cheptels, Exploitations, Productions.

Phalan, B., Balmford, A., Green, R.E., Scharlemann, J.P.W., 2010. Minimising the harm to biodiversity of producing more food globally. J. Food Policy 36, S62–S71. https://doi.org/10.1016/j.foodpol.2010.11.008.

Phalan, B., Onial, M., Balmford, A., Green, R.E., 2011. Reconciling Food Production and Biodiversity Conservation: Land Sharing and Land Sparing Compared. Science 333, 1289–1291. https://doi.org/10.1126/science.1208742.

Polasky, S., Nelson, E., Camm, J., Csuti, B., Fackler, P., Lonsdorf, E., Montgomery, C., White, D., Arthur, J., Garber-Yonts, B., Haight, R., Kagan, J., Starfield, A., Tobalske, C., 2008. Where to put things? Spatial land management to sustain biodiversity and economic returns. Biol. Conserv. 141, 1505–1524. https://doi.org/10.1016/j.biocon.2008.03.022.

Power, A.G., 2010. Ecosystem services and agriculture: tradeoffs and synergies. Philos. Trans. R. Soc. B Biol. Sci. 365, 2959–2971. https://doi.org/10.1098/rstb.2010.0143.

Princé, K., Lorrillière, R., Barbet-Massin, M., Jiguet, F., 2013. Predicting the fate of French bird communities under agriculture and climate change scenarios. Environ. Sci. Pol. 33, 120–132. https://doi.org/10.1016/j.envsci.2013.04.009.

Princé, K., Lorrillière, R., Barbet-Massin, M., Léger, F., Jiguet, F., 2015. Forecasting the effects of land use scenarios on farmland birds reveal a potential mitigation of climate change impacts. PLoS One 10, e0117850. https://doi.org/10.1371/journal.pone.0117850.

Ramankutty, N., Evan, A.T., Monfreda, C., Foley, J.A., 2008. Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. Global Biogeochem. Cycle 22, GB1003. https://doi.org/10.1029/2007GB002952.

Raudsepp-Hearne, C., Peterson, G.D., Bennett, E.M., 2010. Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. Proc. Natl. Acad. Sci. 107, 5242–5247. https://doi.org/10.1073/pnas.0907284107.

Ravetto Enri, S., Probo, M., Farruggia, A., Lanore, L., Blanchetete, A., Dumont, B., 2017. A biodiversity-friendly rotational grazing system enhancing flower-visiting insect assemblages while maintaining animal and grassland productivity. Agric. Ecosyst. Environ. 241, 1–10. https://doi.org/10.1016/j.agee.2017.02.030.

Rodríguez-Ortega, T., Oteros-Rozas, E., Ripoll-Bosch, R., Tichit, M., Martín-López, B., Bernués, A., 2014. Applying the ecosystem services framework to pasture-based livestock farming systems in Europe. Animal 8, 1361–1372. https://doi.org/10.1017/S1751731114000421.

Ruijs, A., Wossink, A., Kortelainen, M., Alkemade, R., Schulp, C.J.E., 2013. Trade-off analysis of ecosystem services in Eastern Europe. Ecosyst. Serv. 4, 82–94. https://doi.org/10.1016/j.ecoser.2013.04.002.

Sabatier, R., Teillard, F., Rossing, W.A.H., Doyen, L., Tichit, M., 2015. Trade-offs between pasture production and farmland bird conservation: exploration of options using a dynamic farm model. Animal 9, 899–907. https://doi.org/10.1017/S175173111400281X.

Seppelt, R., Lautenbach, S., Volk, M., 2013. Identifying trade-offs between ecosystem services, land use, and biodiversity: a plea for combining scenario analysis and optimization on different spatial scales. Curr. Opin. Environ. Sustain. 5, 458–463.

Soussana, J.-F., Lemaire, G., 2014. Coupling carbon and nitrogen cycles for environmentally sustainable intensification of grassland and crop-livestock systems. Agric. Ecosyst. Environ. 190, 9–17. https://doi.org/10.1016/j.agee.2013.10.012.

Soussana, J.-F., Loiseau, P., Vuichard, N., Ceschia, E., Balesdent, J., Chevallier, T., Arrouays, D., 2004. Carbon cycling and sequestration opportunities in temperate grasslands. Soil Use Manag. 20, 219–230. https://doi.org/10.1079/SUM2003234.

Sutherland, W.J., Armstrong-Brown, S., Armsworth, P.R., Brereton, T., Brickland, J., Campbell, C.D., Chamberlain, D.E., Cooke, A.I., Dulvy, N.K., Dusic, N.R., Fitton, M., Freckleton, R.P., Godfray, H.C.J., Grout, N., Harvey, H.J., Hedley, C., Hopkins, J.J., Kift, N.B., Kirby, J., Kunin, W.E., MacDonald, D.W., Marker, B., Naura, M., Neale, A.R., Oliver, T., Osborn, D., Pullin, A.S., Shardlow, M.E.A., Showler, D.A., Smith, P.L., Smithers, R.J., Solandt, J.L., Spencer, J., Spray, C.J., Thomas, C.D., Thompson, J., Webb, S.E., Yalden, D.W., Watkinson, A.R., 2006. The identification of 100 ecological questions of high policy relevance in the UK. J. Appl. Ecol. 43, 617–627. https://doi.org/10.1111/j.1365-2664.2006.01188.x.

Tallis, H., Polasky, S., 2011. Assessing multiple ecosystem services: an integrated tool for the real world. In: Kareiva, P.M., Tallis, H., Ricketts, T.H., Daily, G.C., Polasky, S. (Eds.), Natural Capital: Theory and Practice of Mapping Ecosystem Services. Oxford University Press, Oxford, pp. 34–50.

Teillard, F., Allaire, G., Cahuzac, E., Léger, F., Maigné, E., Tichit, M., 2012. A novel method for mapping agricultural intensity reveals its spatial aggregation: Implications for conservation policies. Agric. Ecosyst. Environ. 149, 135–143. https://doi.org/10.1016/j.agee.2011.12.018.

Teillard, F., Jiguet, F., Tichit, M., 2015. The Response of Farmland Bird Communities to Agricultural Intensity as Influenced by Its Spatial Aggregation. PLoS One 10, e0119674. https://doi.org/10.1371/journal.pone.0119674.

Teillard, F., Doyen, L., Dross, C., Jiguet, F., Tichit, M., 2016. Optimal allocations of agricultural intensity reveal win-no loss solutions for food production and biodiversity. Reg. Environ. Chang. 17, 1397–1408. https://doi.org/10.1007/s10113-016-0947-x.

Thornton, P.K., 2010. Livestock production: recent trends, future prospects. Philos. Trans. R. Soc. B Biol. Sci. 365, 2853–2867. https://doi.org/10.1098/rstb.2010.0134.

Tichit, M., Durant, D., Kernéïs, E., 2005a. The role of grazing in creating suitable sward structures for breeding waders in agricultural landscapes. Livest. Prod. Sci. 96, 119–128. https://doi.org/10.1016/j.livprodsci.2005.05.010.

Tichit, M., Renault, O., Potter, T., 2005b. Grazing regime as a tool to assess positive side effects of livestock farming systems on wading birds. Livest. Prod. Sci. 96, 109–117. https://doi.org/10.1016/j.livprodsci.2005.05.011.

Tilman, D., Balzer, C., Hill, J., Befort, B.L., 2011. Global food demand and the sustainable intensification of agriculture. Proc. Natl. Acad. Sci. U. S. A. 108, 20260–20264. https://doi.org/10.1073/pnas.1116437108.

Tsonkova, P., Böhm, C., Quinkenstein, A., Feese, D., 2015. Application of partial order ranking to identify enhancement potentials for the provision of selected ecosystem services by different land use strategies. Agric. Syst. 135, 112–121. https://doi.org/10.1016/j.agsy.2015.01.002.

Van Zanten, H.H.E., Meerburg, B.G., Bikker, P., Herrero, M., De Boer, I.J.M., 2016. Opinion paper: the role of livestock in a sustainable diet: a land-use perspective. Animal 10, 547–549. https://doi.org/10.1017/S1751731115002694.

Veroustraete, F., Sabbe, H., Eerens, H., 2002. Estimation of carbon mass fluxes over Europe using Fix model and Euroflux data. Remote Sens. Environ. 83, 376–399. https://doi.org/10.1016/S0034-4257(02)00043-3.

Zhang, W., Ricketts, T.H., Kremen, C., Carney, K., Swinton, S.M., 2007. Ecosystem services and dis-services to agriculture. Ecol. Econ. 64, 253–260. https://doi.org/10.1016/j.ecolecon.2007.02.024.