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Frédéric Joly, Marc Benoit, Raphaël Martin, Bertrand Dumont

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Frédéric Joly [a,*], Marc Benoit [a], Raphael Martin [b], Bertrand Dumont [a]

[a] Université Clermont Auvergne, INRAE, Vetagro Sup, UMRH, 63122 Saint-Genès-Champanelle, France
[b] Université Clermont Auvergne, INRAE, Vetagro Sup, UMR Ecosystème Prairial, 63000 Clermont-Ferrand, France

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ABSTRACT

How easily can we obtain optimal trade-offs between conflicting ecosystem services (ES)? We studied this question by crossing metrics of optimality and robustness in a model simulating sheep/cattle mixed-grazing (mixed-grazing is grazing by more than one species). We hypothesized that mixed-grazing processes (complementary use of vegetation and parasitism reduction) would improve ES bundles by increasing meat production with limited additional environmental costs. We assessed bundle optimality with a production possibility frontier and robustness through a management density approach (bundles can be obtained by one or several management decisions). We modeled two provisioning and two regulating ESs and confirmed that mixed-grazing can potentially improve the monetary value of bundles. Optimal bundles were the most robust, because of the shape of the biological function driving animal growth, according to the sheep/cattle ratio. This function is hump-shaped with a plateau that buffers small ratio deviations. It makes bundles optimal or quasi-optimal over a wide range of management decisions, which eases their optimization. For this reason, based on the principles of ergonomics and the definition of the adjective *operable* ('capable of being put into use, operation, or practice'), we considered mixed-grazing a 'Biologically Operable' practice.

1. Introduction

Livestock farming systems are facing unprecedented challenges of food security, societal acceptance and environmental sustainability. They need to meet the demand for safe food products and animal welfare, while producing proteins for a world population projected to reach 10 billion by 2050 (World Bank, 2019). They need to reduce pollution such as greenhouse gas emissions to the atmosphere, and nitrogen leaching into water (Steinfeld et al., 2006). They must also reduce their impacts on biodiversity and the land they use, in order to preserve global ecosystem services (ES) (Costanza et al., 2017; Fischer et al., 2014).

Agroecological practices offer a promising pathway to reduce these impacts. Agroecology is a branch of agriculture that aims at making the best use of biological resources and processes, in order to reduce the use of chemical inputs (Altieri, 1989). By using grasslands as the main feed resource in livestock farming systems, and maintaining natural processes, agroecological practices can secure the ability of pastures to provide ESs. Agroecology has therefore a role to play in the ability of livestock farming systems to deliver valuable ES bundles (Dumont et al., 2013; Raudsepp-Hearne et al., 2010).

Diversification of feed resources, animal species and management practices are key agroecological principles in livestock production (Dumont et al., 2013). Mixed-grazing, i.e. pasture grazing by more than one herbivore species, is one application of these principles. For a given animal density per hectare, mixed sheep/cattle grazing enables higher livestock body growth than monospecific grazing (d'Alexis et al., 2014). This increase is important as meat production performances are largely based on animal growth. This growth improvement is obtained through the complementary use of vegetation, which can improve the value of ingested forage, and reduced parasitism (d'Alexis et al., 2014), as sheep and cattle can be infected by different parasitic worm species. For a given plot area and weight growth per hectare, mixed-grazing has therefore the potential to reduce animal density, compared with monospecific grazing. Farmers can this way produce the same amount of meat on a given surface, with less grazing livestock.

The reduced animal density can bring some environmental benefits, such as the decrease in emissions of enteric methane and other GHGs (Fraser et al., 2014), or a decrease in the amount of grass eaten, which will benefit soil coverage and hence erosion prevention. However, we can expect farm management to become more complex, as mixed-

* Corresponding author.
E-mail address: frederic.joly@inrae.fr (F. Joly).

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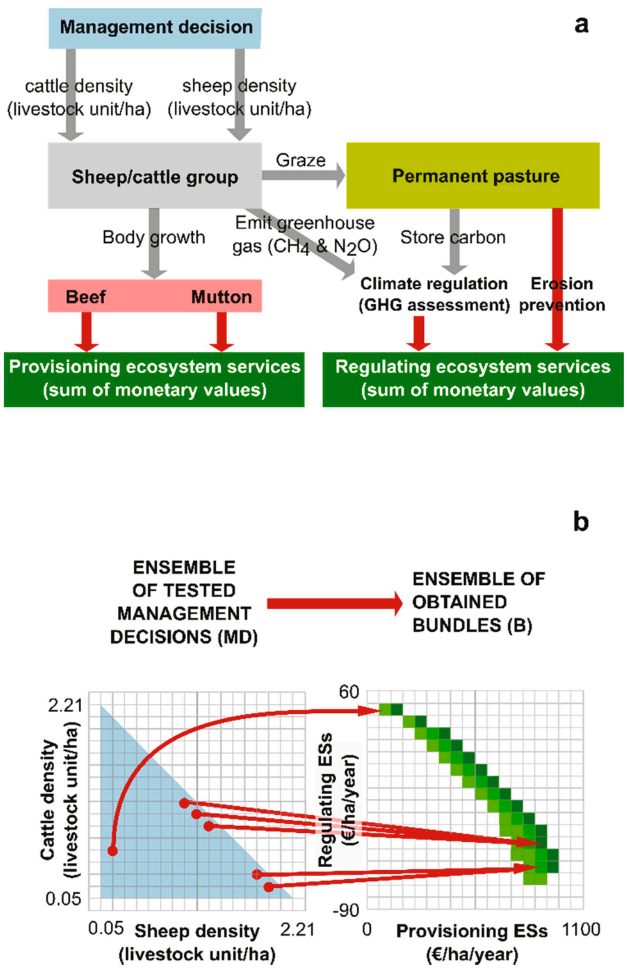

Fig. 1. a: Conceptual model simulating ES bundles according to management decisions. b: Robustness assessment procedure based on the number of management decisions per bundle (shades of green illustrate bundle robustness: the darkest the most robust).

grazing implies technical adaptations and introduces a new parameter: the sheep/cattle ratio.

Here we compared the ecosystem services (ES) bundles provided by sheep/cattle mixed-grazing, against monospecific sheep or cattle grazing. We also addressed the issue of defining sheep/cattle ratio(s) that optimize the ES bundles in mixed-grazing. Studying this question was important as the control of biological processes can be difficult, owing to their complexity (Csete, 2002). Optimizing ES bundles through mixed-grazing processes may therefore require fine-tuning the sheep/cattle ratio, and this management complexity could negatively affect the level of ES delivery (Biggs et al., 2012). To address this question, we used the concept of robustness, which is the ability of a system to maintain its performance in the face of perturbations and uncertainty (Stelling et al., 2004). Applied to management, robustness must ensure satisfactory outcomes despites perturbations and uncertainty, as defined by the robust decision-making concept (Lempert et al., 2010; 2006; Regan et al., 2005). The uncertainty can be external, consisting in climate hazards (Accatino et al., 2014; Sabatier et al., 2015), or internal, consisting in subsystem failure (Csete, 2002). Here we used the second definition, and considered that applying suboptimal sheep/cattle ratios would be a failure to take advantage of mixed-grazing processes.

To assess the pertinence of mixed-grazing in this robustness context, the effect of imperfect management decisions must be evaluated. In this aim, the relationship between the sheep/cattle ratio and the provision of different ESs must be understood. In particular, the pattern of response of the biological variables impacting ESs according to the sheep/cattle ratio must be studied. The ratio optimizing ES bundles must be defined and the consequence of deviations from this ratio assessed. If deviations have a negligible effect on ESs, mixed-grazing has the potential to offer robust decision-making strategies. Oppositely, if deviations result in a strong decrease, mixed-grazing is disqualified.

We tested the effect of different management decisions (animal density per hectare and sheep/cattle ratio) on the supply of multiple ES. We used a modeling approach to simulate all possible decisions and assess the potential of mixed-grazing for improving ES bundles. We hypothesized that mixed-grazing could increase animal performances and hence provisioning ES, with limited impact on regulating ES. We then tested the optimality and robustness of each of the bundles obtained, in order to assess how easily a farmer could deliver the best of them. We hypothesized that the biological pattern of mixed-grazing processes would affect the ease of obtaining the best possible bundles, and thus the robustness of the decision-making. We then used our results to introduce the concept of 'Biological Operability', as a way of characterizing how robustly a livestock farm manager can obtain optimal ES bundles.

2. Materials and methods

2.1. Modeling ES bundles

We developed a model describing the vegetation of a pasture grazed by a group of sheep and cattle (Fig. 1a). This pasture is a permanent pasture, i.e. a pasture that has never been ploughed and sown. It is used during the grazing season, i.e. the milder time of the year when animals can be fed outside on grass. The model simulates livestock body growth (i.e. weight increase), under monospecific or mixed-grazing conditions. It also simulates the impact of animal grazing on aboveground vegetation biomass. From these simulations, we estimated values of provisioning and regulating ES for the whole range of management decisions compatible with grass production (i.e. where the pasture is able to feed animals).

To quantify animal density and its impact on grass consumption, we used livestock units (LU) per hectare ($LU \cdot ha^{-1}$). This made it possible to express sheep and cattle density in a common unit. This livestock unit is a measure of grass intake linked to the energy needs of the animals. We based this unit on the animals' metabolic weight, which is more directly related to animal energy consumption than liveweight (liveweight is the term animal scientists use for the 'normal' weight). Metabolic needs decrease nonlinearly with liveweight, which is why metabolic weight is appropriate for studying different-body size animals (Bakker et al., 2004; Demment and Van Soest, 1985). Following Allen et al. (2011) and Dumont et al. (2007), we used in this study a livestock unit of 600 kg of liveweight. This definition is expressed by Eq. 1, where *AD* is animal density in LU (*AD* is equivalent to the 'stocking rate' of livestock scientists).

$$AD = (Liveweight/600)^{0.75} \quad (1)$$

We quantified ES from the supply side according to pasture and animal characteristics, using the economic value generated per year. Provisioning ESs are sheep and cattle meat production, and regulating ESs are climate mitigation and erosion prevention. We obtained this way bundles of four ESs of interest in a livestock farming context (Dumont et al., 2019). Meat ES is assessed from the increase in liveweight of young animals that are in their growth stage, and intended for sale. Erosion prevention is assessed from the residual grass biomass at end of the grazing of this season. Climate regulation is based on the balance between GHGs emitted by the animals, and carbon stored in the pasture. We aggregated the two provisioning and two regulating ESs by summing their monetary values to obtain one pair of ESs per management decision. We thus obtained X and Y coordinates to visualize the assemblage

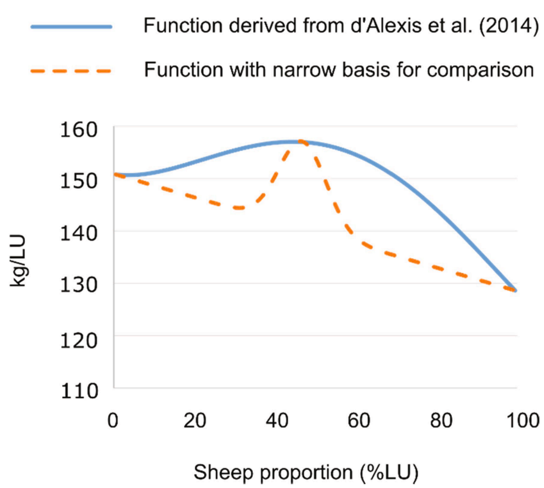

Fig. 2. Functions of animal weight increase (kg) per livestock unit (LU) during the grazing season, according to the sheep/cattle group composition expressed in LU (both functions peaks at identical values).

of ES bundles in two dimensions (a regulating and a provisioning dimension).

The purpose of this model is not to precisely predict ES values but, as above mentioned, to explore robustness of ES bundles according to the biological relationships involved in grazing. Not all these relationships are linear and for instance, the improvement of animal growth per hectare due to mixed-grazing has a flattened hump-shaped structure (d'Alexis et al., 2014). To study the implications of this pattern, we used an equation reproducing its humped shape with sheep and cattle having close growth per livestock unit. We then used a comparative equation providing the same maximal animal growth improvement per hectare, but without the flattened hump back, and with a narrow basis (Fig. 2). From this comparison, we assessed whether the flattened hump-shaped pattern could help farmers find robust management decisions maximizing animal growth, in order to optimize ES bundles.

2.2. Modeling the response of ES bundles to management decisions

The response of ES bundles to management decisions is expressed by Eq. 2

$$b_j = f(md_i) \tag{2}$$

where md_i and b_j are two-dimensional vectors representing the management decision i and the ES bundle j delivered by this decision, respectively. They are both discretized and md_i stands for the vector $\begin{pmatrix} AD_{cattle,i} \\ AD_{sheep,i} \end{pmatrix}$, where $AD_{cattle,i}$ and $AD_{sheep,i}$ are animal density of cattle and sheep in management decision i, in livestock units per hectare ($LU{\cdot}ha^{-1}$). b_j stands for the vector $\begin{pmatrix} ESp_j \\ ESr_j \end{pmatrix}$, where ESp_j and ESr_j represent the value of provisioning and regulating ESs, respectively. ESp_j and ESr_j are defined by the upper and lower intervals of their monetary value, as illustrated in Fig. 1b. With this discretization configuration (discrete value for *md* and interval of discrete values for *b*), a given bundle can be obtained by one decision or more (Fig. 1b). For example, a given meat value per ha can result from one or more animal group compositions. There are therefore more management decisions possible than obtainable bundles, which is why we attributed distinct indices to *md* and *b* (resp. *i* and *j*).

We tested a large number of management decisions on a gradient of animal densities ranging from the minimum required to prevent afforestation, set to 0.1 $LU{\cdot}ha^{-1}$, up to the maximum imposed by the amount of grass produced by the pasture. This value is based on grass consumption per livestock unit and is equal to 2.26 $LU{\cdot}ha^{-1}$ (calculation detailed in appendix A). To respect this overall animal density range, individual species density ranges from 0.05 to 2.21 $LU{\cdot}ha^{-1}$ for both sheep and cattle, with an interval of 0.00108 $LU{\cdot}ha^{-1}$ (bounding to 2.21 prevents the sum of species densities to exceed 2.26 $LU{\cdot}ha^{-1}$). We tested this way a total of around 2 million management decisions that constitute MD, the ensemble of all possible decisions (Fig. 1b).

From MD, we identified B, the ensemble of all possible obtainable bundles (Eq. 3). These bundles were distributed along a gradient of regulating ES values ranging from €-90 to €60, at €0.75 intervals, and along a gradient of provisioning ES values ranging from €0 to €1100, at €5.5 intervals. These values were identified through initial trials and we tested this way a total of 40,000 possible bundles.

$$B = f(\mathrm{MD}) \tag{3}$$

2.3. Bundles optimality and robustness

To assess the robustness and optimality of bundles, we crossed metrics related to these properties. This approach has been applied in a similar context (robustness and optimality of trade-offs between production and biodiversity in farmlands) by Sabatier and Mouysset (2018). To quantify the robustness of a given bundle b_j, we used an approach based on management density. We first computed $P(b_j)$, the probability of obtaining b_j by randomly choosing a management decision (Eq. 4):

$$P(b_j) = Card(MD_{\{b_j\}}) / \mathrm{Card(MD)} \tag{4}$$

where $Card(MD_{\{b_j\}})$ is the number of tested management decisions delivering bundle b_j and Card(MD) the overall number of decisions tested. We then expressed $R(b_j)$, the robustness of b_j, as the relative probability of obtaining the bundle. This probability is relative to the average probability of obtaining the bundles constituting B, as expressed by Eq. 5. We used this expression as we considered a relative probability more intuitive and easy to interpret than a raw probability. A value above 1 indicates a bundle more likely to be obtained than the average bundle, and a value below 1 indicates a bundle less likely to be obtained.

$$R(b_j) = P(b_j) / \overline{\mathrm{P(b_j)}_{b_j \in B}} \tag{5}$$

where $\overline{\mathrm{P(b_j)}_{b_j \in B}}$ is the mean probability of obtaining b_j in B.

We then assessed bundle optimality based on whether it belongs to the production possibility frontier (PPF), in accordance with Vallet et al. (2018). A bundle b_k is optimal if it belongs to the PPF, where there is no other bundle j, for which ESp_j and ESr_j are both superior. We further characterized the PPF by calculating the mean value of its bundles, which helped us quantify the overall potential of improvement of mixed-grazing. The resulting value, noted V(PPF), is expressed through Eq. 6.

$$\mathrm{V(PPF)} = \frac{1}{\mathrm{Card(PPF)}} \sum_{b_k \in \mathrm{PPF}} (ESp_k + ESr_k) \tag{6}$$

where Card(PPF) is the number of bundles in PPF.

The equations quantifying animal growth, vegetation biomass and ESs are given in appendix A. The model was parameterized based on data for the North of *Massif Central* uplands (central France). The sources used for the parameterization are also given in appendix A.

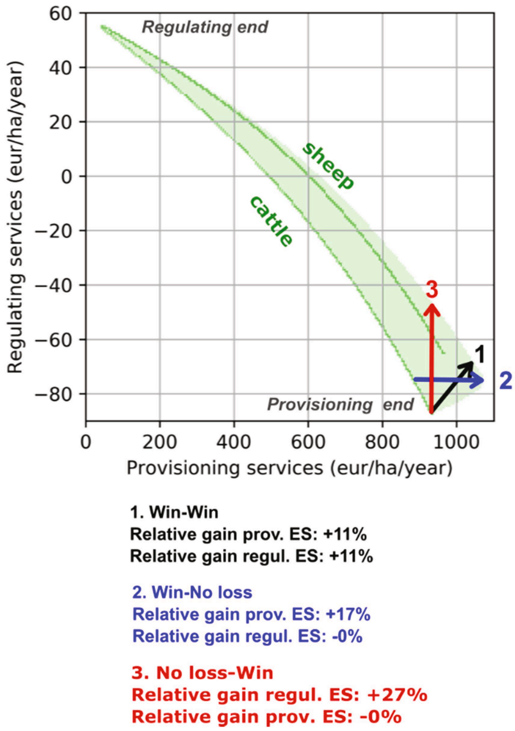

Fig. 3. Bundles provided by monospecific groups of sheep and cattle (dark plain lines) and by mixed-groups (light green space) (bundles based on the weight increase function from d'Alexis et al. (2014)). The arrows give examples of relative gains and losses occurring when switching from large monospecific cattle herds (the most common in the study area) to other mixed-species groups.

2.4. Simulations

We first ran a simulation with the two types of monospecific sheep and cattle groups. Animal density ranged from 0.1 to 2.26 for both species, with the same density interval as for the mixed-species groups. We then ran a simulation with all mixed-species groups in MD, using the real equation of mixed-grazing liveweight growth improvement (derived from d'Alexis et al., 2014). We thus assessed the improvement of bundles from monospecific to mixed-grazing. We then ran a simulation with all mixed-species groups in MD, with the comparative equation of mixed-species grazing from Fig. 2. This procedure enabled us to assess how the pattern of the mixed-grazing process shapes the robustness of optimal bundles.

2.5. Sensitivity analysis

We used some ES monetary values in our model that are not from *Massif Central*, but from comparable contexts (see the Parameterization section in Appendix A). To assess possible 'value transfer' biases, i.e. biases occurring when valuating ES in one site from data from another one (Plummer, 2009), we ran a sensitivity analysis. We first modified our four ES values individually, in a 'one-at-a-time' analysis. We then modified the regulating and provisioning services at the same time, assuming that the demands for a given type of services (regulating or provisioning) would be correlated. We did it assuming that climate change would increase demand for both regulating services at the same time, or decrease consumer demand for both types of meat (both cause greenhouse gas emissions). All simulations in this analysis were made with the real weight function derived from d'Alexis et al. (2014).

2.6. Code availability

The model was written in Python 3.7, and the code is available at https://doi.org//10.15454/X3OCET.

3. Results

3.1. Ensemble of obtainable ES bundles

The ES bundles generated by the two monospecific sheep and cattle groups are distributed along convex curves, that express an antagonism between regulating and provisioning ESs (Fig. 3). This convexity is due to the non-linearity of the ES responses, according to animal density (see Appendix A). The upper left tip of the curves represents a 'regulating end' corresponding to small groups of animals, i.e. groups with low animal density (Fig. 3). These configurations generate little animal growth per hectare, which creates a modest value in terms of provisioning ES. They leave sufficient vegetation to ensure a high level of erosion prevention, emit low amounts of GHGs, and store high levels of soil carbon, thereby contributing significantly to climate regulation. These small group configurations thus generate high regulating ES values. In contrast, the lower right tip of the curves represents a 'provisioning end' (Fig. 3) that corresponds to large groups of animals, i.e groups with high animal density. These groups generate high levels of provisioning ES and low levels of regulating ES. The PPF of this pair of monospecific grazing groups would match the sheep curve, as the cattle curve is always below the sheep one (Fig. 3). The value of the sheep curve is higher than that of cattle, despite a slightly lower weight increase of sheep compared to cattle (Fig. 2). This is due to the higher price of mutton compared to beef (Table A.1 - Appendix A).

The bundles obtained by scanning all possible mixed-grazing management decisions, with the real growth function derived from d'Alexis et al. (2014), form a convex curved ensemble, expressing the same antagonism between regulating and provisioning ESs (Fig. 3). This ensemble fills the area between the two monospecific curves and spreads into an area at the right of the sheep curve. This spread indicates that mixed-grazing increases the maximum possible value of the provisioning ESs (by 12%), with limited effect on the regulating ES range (minimum and maximum regulating ES values changed by less than 1%). As a result, the mean bundle value along the whole PPF is €603.12 in mixed grazing, against €545.32 in monospecific grazing ('PPF' of monospecific groups is the monospecific sheep curve). This represents a 10.59% increase.

The PPF bundles were obtained by applying management decisions corresponding to fairly balanced groups, with around 66% LU of sheep, as illustrated in Fig. 4c (groups obtained by identifying all management decisions providing PPF bundles with the help of the model). In heads, it corresponds to approximately one head of cattle for ten head of sheep (1 LU corresponds to 7.37 head of sheep and 1.28 head of cattle with our parameters–see Appendix A).

3.2. Structure of trade-offs between ESs

The shape of the bundle ensemble helps quantify the gains and losses obtained by transitioning from one bundle to another (Fig. 3). These gains can be quantified in terms of relative gains and losses over a range of ES values (e.g. differences of ±€15 euros on a gradient with minimal and maximal values differing by €150 euros have relative changes of ± 10%). It is of particular interest to study the gains obtained from transitioning from bundles offered the by most common animal groups in the study area, to other types of group. These most common groups are rather similar to the biggest cattle herds we tested (Benoit and Lherm,

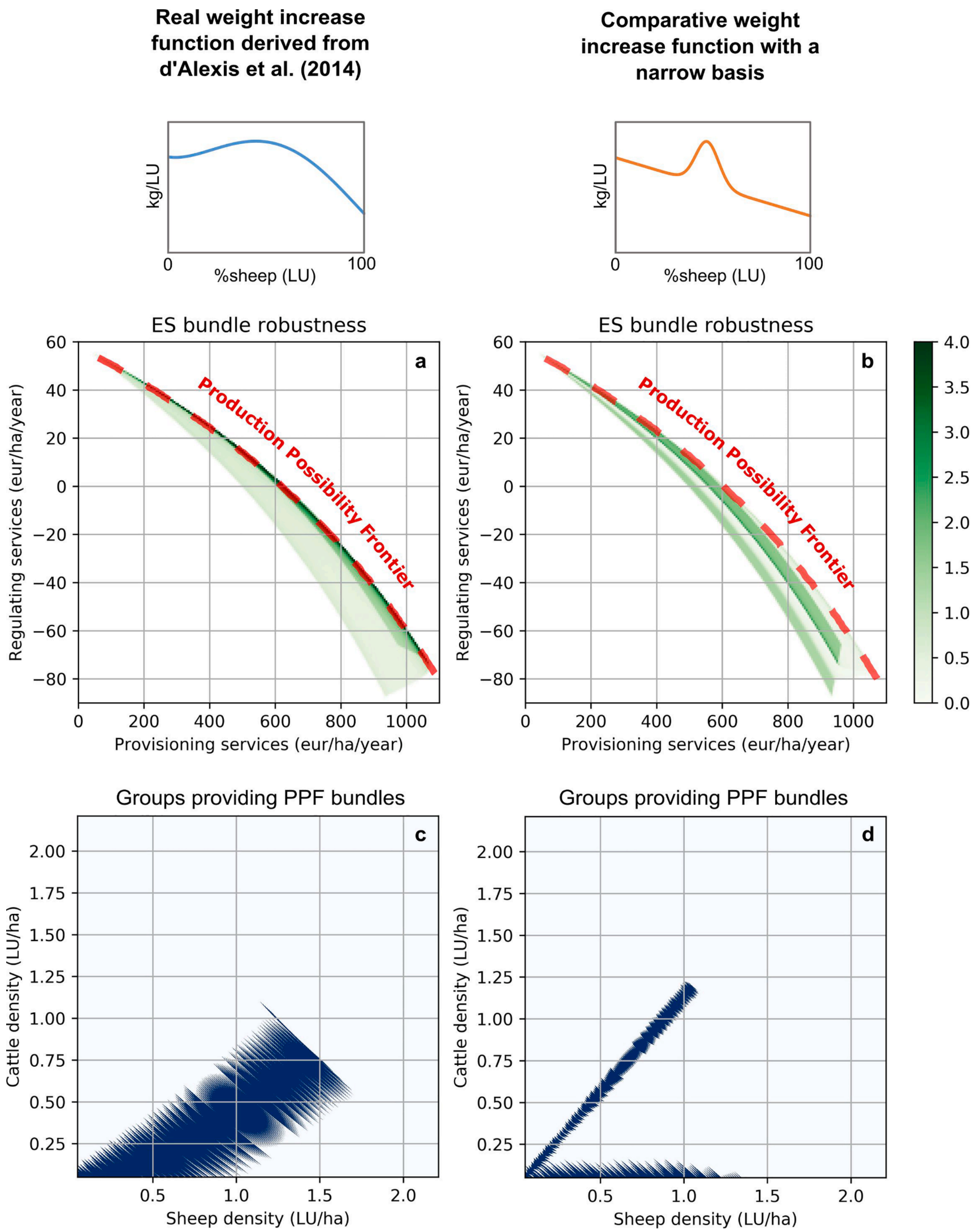

Fig. 4. Ensemble of ecosystem service bundles in mixed-species groups according to the weight increase function used (a and b). Shades of green represent the robustness of the bundles, defined as the relative probability of obtaining them: a robustness > 1 represents a bundle that is more likely to get than the average bundle (the darkest the most robust). Values above 4 are merged and represented by the darkest shade of green for visibility. Production possibility frontier (PPF) of bundle ensembles are represented by red dotted lines. Sheep/cattle groups providing PPF bundles are given in c and d.

2018), grazing at 2.26 LU·ha^{-1} over the grazing season. Transitioning from them to certain mixed configurations can offer gains of 11% on the PPF, in both regulating and provisioning services in a win/win transition (this 11% is close but distinct from the 10.59% increase of the mean PPF bundle value from monospecific to mixed-grazing). The curves also show that other transitions, starting from big cattle groups, can provide a gain of 17% in provisioning services, without degrading the regulating services, in a win/no-lose way. It is equally possible to obtain a no-lose/win transition maintaining provisioning ESs, while increasing regulation ESs by an important 27%.

3.3. Robustness of ES bundles

In terms of robustness of the mixed grazing bundles, there is a gradient perpendicular to the provisioning/regulating gradient (shades of green in Fig. 4a). The highest robustness corresponds to bundles on the PPF, or just below the PPF. The mean robustness of PPF bundles is 3.23, which means that, according to our definition of robustness, PPF bundles are 3.23 times more likely to be obtained than the average bundle. Entering the narrow-basis comparative growth function into the model inverted the robustness pattern (Fig. 4b). The areas of highest robustness were found with this function at the immediate proximity of the monospecific sheep and cattle curves, as seen by comparing Figs. 3 and 4b. The robustness around PPF was among the lowest, with mean PPF robustness falling to 0.76. These differences in robustness are due to the more or less important number of herds delivering an optimal bundle, as illustrated by comparing Fig. 4c with 4d. Note too that with the narrow basis curve simulation, some of the PPF bundles were generated from small monospecific sheep flocks (bottom of Fig. 4d). This is because PPF bundles of mixed-grazing and PPF bundles of sheep flocks converge on the regulating end of the bundle ensemble.

3.4. Sensitivity analysis

The sensitivity analysis (Appendix B) indicates that the convex shape of the bundle ensemble is stable. It also shows that PPF robustness never falls below 2.41, meaning that even in the worst-case scenario, these bundles remain 2.41 times more likely to be obtained than the average bundle. The analysis also indicates that in most ES value scenarios, the management decisions that produce PPF bundles involve fairly balanced mixed groups. It also shows that in most scenarios, transitioning from monospecific to mixed grazing generates an increase of mean PPF monetary value roughly revolving around 10.5% (Table B.1). Animal groups providing PPF bundles, and increases of PPF value only differ from this pattern in ES value scenarios with individual changes in beef or mutton prices, in the 'one-at-a-time' analysis (mean PPF monetary value only increases from 0.79% to 3.55%). Indeed, if one meat becomes far more profitable than the other one, all of the productive benefits of mixing cattle and sheep are lost. However, unless a major health issue such as the mad cow disease outbreak in the 1990 s happens, there is no reason to expect a big change in meat price for just a single species. Surveys show that local mutton and beef prices are rather stable since 1995 (Veysset et al., 2014). We therefore considered the patterns described in our results relevant.

4. Discussion

4.1. Assessment of mixed-grazing as an optimization practice

For four target ESs, we identified all possible bundles resulting from monospecific or mixed-grazing. These bundles form an ensemble illustrating the structure of relationships between ESs, which is useful for assessing the interest of mixed-grazing to improve ES bundles. First, the ensemble confirms the classical antagonism between regulating and provisioning ES, reported in various situations and scales (Dumont et al., 2019; Kong et al., 2018; Lee and Lautenbach, 2016; Maes et al., 2012; Turner et al., 2014). This antagonism is further characterized by the convex shape of the state space, which expresses a low level of conflict (Müller et al., 2016).

Second, the ensemble shows that mixed-grazing can return a 10.59% increase in value of PPF bundles, compared to monospecific grazing. This increase is obtained through an improvement of provisioning ESs value, which is higher than the decrease in regulating ESs. This result supports our first hypothesis that mixed-grazing has the potential to improve productive performances, with limited environmental impact. The ensemble also reveals that targeting the PPF can produce win–win transitions, as well as a number of no-lose/win transitions. It shows that substantial gains of up to 27% in regulating ESs can be expected, by transitioning from the usual monospecific cattle herd types of the area to certain mixed-groups, without degrading the level of provisioning ESs. Such gain results from the improved weight increase of mixed groups, compared to monospecific ones. A given animal liveweight increase per ha for the animal group, and at the pasture scale, is hence obtained from mixed groups that are smaller than monospecific ones. This reduced animal density, and resulting reduced grazing intensity, improves soil protection from vegetation and reduces GHG emissions, thereby improving the value of regulating ESs. The model indicates that this gain can be obtained, for example, by transitioning from a monospecific cattle herd at 2.26 LU·ha^{-1} (i.e. similar to the most common herds of the study area) to a mixed group with sheep and cattle at densities of 1.3 and 0.65 LU·ha^{-1}, respectively. This is equivalent to approximately 95 head of sheep and 8 head of cattle, grazing a 10 ha pasture for 180 days.

Finally, the ensemble shows, through our robustness metric, that PPF bundles are easy to obtain when using the flat hump-shaped function derived from d'Alexis et al. (2014). It therefore suggests that optimizing bundles is a realistic management objective. However, the sensitivity analysis found that the gain of mixed-grazing disappears if one species becomes much more profitable than the other. In such case, it makes more sense to focus on the most profitable species.

Thus, to summarize, the ensemble produced by our model suggests that mixed-grazing can improve the value of optimal ES bundles, provided that the profitability sheep and cattle do not differ too much. These optimal bundles are in addition robust, which points towards a real potential of mixed-grazing as an optimization practice. A notable interest of mixed-grazing is the improvement of the value of regulating ESs, with no decrease of the value of provisioning ESs. Mixed-grazing implementation could therefore be motivated by a monetized market for regulating ESs (it does not exist for the moment).

4.2. Limits and future improvement

The approach we used to describe ES bundles could be improved and a first way concerns the 'value transfer' approach we used to assess ESs. The sensitivity analysis showed that it does not affect our results on robustness, and has only modest impact on PPF value improvement from mixed-grazing. However, it obviously affects the modeled bundle values. A first easy way to address this issue would be to update our model parameters, when data pertaining our study region becomes available. A second way would be to use direct biophysical values to assess ESs, for example from the amount of meat produced, or CO_2 equivalents emitted. However, this second option would require visualization tools in dimensions above 2, as it would prevent aggregation of values expressed in different units (e.g. kg of meat and CO_2 equivalents cannot be summed).

Developing such tools represents the second way of improvement of our approach. For the ease of visualization, we used a 2D representation of aggregated monetary value of provisioning and regulating services. This kind of 2D visualization is common (Bekele et al., 2013; Kragt and Robertson, 2014; Lautenbach et al., 2013; Müller et al., 2016), but restrains the capability of displaying all the antagonisms between all the 4 modeled ESs. Further developments include the disaggregation of the services and the analysis of 3D, or higher dimensions production frontiers. The metrics of robustness and optimality we used are compatible with such higher dimensionality, and would also offer the possibility of adding cultural ESs, for example. However, it would add complexity to the visual interpretation of model results. The convexity or concavity of bundle ensembles, which has an impact on the degree of conflict between provisioning and regulating ESs, would become in addition more difficult to assess. Analysis of such model outputs could be facilitated by developing intuitive metrics and visualization tools compatible with representations in dimensions above two.

4.3. Bundle robustness

We found that optimal bundles are the most robust, which can seem counter-intuitive. We can explain it by the function describing animal growth, derived from d'Alexis et al. (2014). This function has a flattened hump-backed shape with a wide basis, which means that it has a plateau around its peak value. This plateau buffers management decisions that are suboptimal, because minor deviations from the peak ratio still provide optimal or near-optimal bundles. In contrast, the alternative function with a narrow basis delivers far fewer PPF bundles. Obtaining optimal bundles with this function therefore requires targeting precisely the peak ratio, which means that management decisions need to be fine-tuned. The shape of the biological function driving animal performances therefore dictates the tolerance to small decision imperfections: high when there is a plateau around the peak ratio, and low when the curve has a narrow basis. This finding confirms our second hypothesis that the biological pattern of mixed-grazing processes affects the ease of obtaining optimal bundles. It also illustrates how the pattern of biological response to a management parameter influences the possibility to implement a robust decision-making strategy.

These findings are valuable for assessing whether a biological process is a good ally for optimizing ES bundles. They can inspire the development of a concept for leading this assessment. The concept could be derived from cognitive ergonomics, a discipline that helps operators to optimize the use of complex machines (Long, 2000). Cognitive ergonomics argues that operators should not be overwhelmed by information and workload, to avoid failures (Cardoso and Fernandes, 2011; Haramina et al., 2009; O'Hare et al., 1994). In this regard, a bundle optimization procedure should not entail tedious monitoring and adjustment procedures, or extensive data processing. The results of our modeling indicate that mixed-grazing fulfills these criteria, as it tolerates small deviations from the sheep/cattle optimal peak ratio. It eliminates this way the need for continuous monitoring and corrective adjustments of small deviations from the peak ratio. It thereby leaves the farmer free to focus on other livestock farming tasks. Of course, this assessment does not account for the technical and organizational constraints of mixed-grazing (e.g. specific fencing), but it clearly suggests that from a biological viewpoint, and from a cognitive ergonomics perspective, mixed-grazing has clear advantages. Based on the definition of the adjective operable ('capable of being put into use, operation, or practice' (Dictionary.com, 2020)), we therefore consider mixed-grazing a 'Biologically Operable' practice.

5. Conclusion

In this research, we assessed how easily a farmer could obtain optimal ES bundles by implementing a specific management practice. We crossed metrics of robustness and optimality and showed that optimal bundles are not obligatorily the most difficult to get. To understand this result, we studied the biological patterns of response of ES to management decisions. We then described the relationship between these patterns and the tolerance to imperfect management decisions. To the best of our knowledge, it is the first time this relationship is studied.

Based on the principles of cognitive ergonomics, we proposed the concept of Biological Operability to illustrate the pertinence of an optimization practice. We focused on the tolerance to imperfect management decisions and the capability to buffer their effects. We considered this tolerance a factor of robustness and an advantage from a practical point of view, as it reduces the need for extensive monitoring and adjusting procedures.

Our concept of Biological Operability could be further developed by taking into accounts other aspects. Further developments includes the robustness to external uncertainty, such as climate, and the duration of efficiency of a solution (e.g. a bio-regulator may only be efficient under certain weather conditions and during a specific period of the year). The Biological Operability concept could be applied to future nature-based and agroecological practices of ES bundles optimization, together with an assessment of their technical constraints (e.g. 'technical operability'), to assess their operational validity and practical potential.

Declaration of Competing Interest

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

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Appendix A:. Plant and animal dynamics

Animal liveweight gain

The animal model simulates the liveweight gain (LWG) of young animals in their growth stage, according to the overall animal density in the pasture (mother + young animals). We modeled LWG by summing the baseline gain of a monospecific configuration and the gain improvement resulting from mixed grazing. Gain improvement was derived from the literature review of d'Alexis et al. (2014), who established that i) only sheep LWG is improved in mixed-grazing (cattle LWG is unchanged), ii) the maximum increase in sheep LWG in the mixed configuration is + 30%, iii) the mean improvement in animal LWG per ha (sheep + cattle) is + 8%, and iv) improvement of LWG according to sheep/cattle ratio follows a flattened hump-shaped pattern with a wide basis, where the hump peaks for intermediate ratios. This pattern is expressed through Eq. A.1 to Eq. A.4.

$$LWG_{cattle,i} = \mathrm{ULWG}_{\mathrm{cattle}} \cdot AD_{cattle,i} \tag{A.1}$$

$$LWG_{sheep,i} = \mathrm{ULWG}_{\mathrm{sheep}} \cdot AD_{sheep,i} \cdot (1 + \mu \cdot GM(\rho_i)) \tag{A.2}$$

where $LWG_{cattle,i}$ and $LWG_{sheep,i}$ are the LWG of cattle and sheep, respectively, in $\mathrm{kg \cdot ha^{-1}}$ obtained through management decision md_i that specifies the animal density in $\mathrm{LU \cdot ha^{-1}}$ of cattle ($AD_{cattle,i}$) and sheep ($AD_{sheep,i}$). $\mathrm{ULWG}_{\mathrm{cattle}}$ and $\mathrm{ULWG}_{\mathrm{sheep}}$ are the amount of LW produced by one LU over the study period in a monospecific configuration, and μ is the potential gain of mixed grazing for sheep. $GM(\rho_i)$ is a gain factor, and ρ_i is the proportion of sheep in the total animal density, expressed by Eq. A.3. $GM(\rho_i)$ is expressed through Eq. A.4 and was obtained through a series of manual adjustments to fit the criteria of d'Alexis et al. (2014).

$$\rho_i = AD_{sheep,i} / (AD_{cattle,i} + AD_{sheep,i}) \tag{A.3}$$

$$GM(\rho_i) = 3.34\rho_i^3 - 7.86\rho_i^2 + 4.18\rho_i + 0.34 \tag{A.4}$$

The comparative function that provides the same maximum LWG per LU per ha than d'Alexis et al. (2014), but differs from its pattern (with a narrow basis) is expressed by Eq. A.4′.

$$GM(\rho_i) = 0.93 \cdot \exp(-0.5 \cdot ((\rho_i - 0.46)/0.05)^2)) \tag{A.4′}$$

There is no effect of animal density on LWG in the model, because the grass allocated to livestock remains within the limit established by the technical reference of Hulin et al. (2010). The maximum tested density is based on the potential usable biomass for grazing (PUB) of 5300 kg/ha, leaving sufficient standing grass to prevent animal grass intake decrease (Jouven et al., 2008) (see sections 'Animal grazing' and 'Maximum animal density tested'). We therefore considered that animals would not be limited from an intake standpoint.

Animal grazing

We described pasture state using RAB_i, the residual usable aboveground biomass (in $kg \cdot ha^{-1}$) at the end of the grazing season, after grazing by an animal group of a given composition (as determined by md_i) (Eq. A.5):

$$RAB_i = \mathrm{PUB} - (AD_{cattle,i} + AD_{sheep,i} \cdot (1 + (\mathrm{ULWG_{sheep}}/600) \cdot \mu \cdot GM(\rho_i)/2)^{0.75}) \cdot \mathrm{C_{LU}} \cdot \mathrm{D} \tag{A.5}$$

where $\mathrm{C_{LU}}$ is the dry matter consumption of one LU per day in $kg \cdot LU^{-1} \cdot day^{-1}$, and D is the duration of the grazing season in days (the same for all management decisions tested). The term $(1 + (\mathrm{ULWG_{sheep}}/600) \cdot \mu \cdot GM(\rho_i)/2)^{0.75}$ accounts for the effect of the additional sheep metabolic weight on forage consumption in mixed-grazing groups. $(\mathrm{ULWG_{sheep}}/600) \cdot \mu \cdot GM(\rho_i)$is divided by 2 in order to take the mean additional animal weight, between the start and end of the season (considering linear growth).

Assessment of ES bundles

Provisioning services

Provisioning services were assessed by meat production through the price of livestock (Eq. A.6):

$$ESp_i = LWG_{cattle,i} \cdot \mathrm{P_{cattle}} + LWG_{sheep,i} \cdot \mathrm{P_{sheep}} \tag{A.6}$$

where $\mathrm{P_{cattle}}$ and $\mathrm{P_{sheep}}$ are the prices for one kg of liveweight of cattle and sheep in $eur \cdot kg^{-1}$. Let's note that this equation expresses *ESp* according to indice *i* because it corresponds to the situation where the bundles *b* have not yet been distributed along the discretized ensemble *B* (remark valid for *ESr* below as well).

Regulating services

Regulating service ESr_i is the sum of $ESr_{e,i}$ and $ESr_{c,i}$, the monetary values of erosion prevention ES and climate regulation ES, respectively (Eq. A.7).

$$ESr_i = ESr_{e,i} + ESr_{c,i} \tag{A.7}$$

In accordance with Sattler et al. (2013), these regulating ESs were assessed through the additional gains provided by md_i compared with an ES baseline scenario. This baseline scenario corresponds to a situation where PUB is entirely allocated to provisioning ES (livestock production). This quantification differs from that of the provisioning ESs, which is directly assessed from animal LWG. This is due to the fact that there is a formal market for meat, whereas there is none for regulating services. However, this quantification does not conflict with our purpose of assessing ES bundles changes, in response to mixed-grazing. This aim entails describing how an ES change by comparison with other ESs. To do this we need to quantify the relative modifications in ES values according to our management drivers (animal density and sheep/cattle ratio), and not specific ES values. Using a direct valuation method, together with a comparative method, is therefore compatible with this approach.

Erosion prevention

The erosion prevention ES is widely studied via the RUSLE model (Estrada-Carmona et al., 2017; Schmidt et al., 2019; Xue et al., 2018). This model assesses the amount of soil lost over a year due to rainfall according to topography, soil texture and land use (Renard et al., 1991). Land use impacts erosion through the efficiency of vegetation in protecting soil, which is why vegetation cover is used to assess the erosion prevention services (Petz et al., 2014). This is quantified here using pasture biomass (i.e. the residual aboveground biomass) as a proxy, as both variables are correlated (Axmanová et al., 2012; Ónodi et al., 2017; Pordel et al., 2018).

We used an equation to normalize the range of RAB_i to a valuating service coefficient η (Eq. A.8). This equation accounts for the nonlinear relationship between biomass and cover in a European mesic context, and reproduces the curved pattern reported by Axmanová et al. (2012) and Ónodi et al. (2017). The range of RAB_i goes from 0 to almost PUB, with 0 being the regulating ES baseline scenario (PUB is never completely attained because we did not simulate a no-livestock scenario).

$$ESr_{e,i} = \eta \cdot (1 - (1 - RAB_i/\mathrm{PUB})^3) \tag{A.8}$$

Climate regulation

We assessed the climate regulation service via an annual greenhouse gas (GHG) assessment. It takes into account carbon sequestration by the pasture, enteric CH_4 emissions, and CH_4 and N_2O emissions from manure (for manure, we considered all animal wastes in accordance with IPCC (2006)). CH_4 and N_2O emissions were estimated through the IPCC tier-1 equations and carbon sequestration was assessed through a comparative approach, derived from Searchinger et al. (2018). In this approach, we used our baseline scenario, where PUB is entirely consumed by livestock, and compared it with the rest of the modeled management decisions. The difference in carbon stocks was divided by a 100-year reference period (as in Searchinger et al., 2018) to convert stocks into annual fluxes. Stocks were assessed as per IPCC (2006) guidelines (tier 2) that recommend studying five pasture compartments: above and belowground biomass, soil organic carbon (SOC), dead wood, and litter. Here we focused on the first three compartments, as dead wood and litter are not relevant in our bioclimatic context. Local livestock farming pastures are indeed mostly made of herbaceous species (Dumont et al., 2011) and litter does not accumulate over years (Loiseau et al., 1998).

The GHG assessment is expressed for md_i through Eq. A.9:

$$ESr_{c,i} = \tau \cdot (S_i - E_i) \tag{A.9}$$

where τ, S_i and E_i are market price of a kg of CO_2 on the European allowances market in €, carbon sequestration by pasture and GHG emissions due to livestock, respectively. S_i and E_i are expressed in kg CO_2 equivalents, with E_i expressed through Eq. A.10:

$$E_i = \sum_{l \in \{sheep, cattle\}, m \in \{GHGtype\}} e_{m,l} \cdot eCO2_m \cdot AD_{l,i} \cdot H_l^{LU} \cdot (1 + \left(\frac{ULWG_l}{600}\right) \cdot \mu_l \cdot GM(\rho_i)/2)^{0.75} \cdot D/365 \tag{A.10}$$

where $e_{m,l}$ is the annual emission of GHG of gas type m from one head of species l over a 100-year reference period, $eCO2_m$ and H_l^{LU} are the CO_2 equivalent of GHG emissions of type m and number of head of animals of species l per LU, respectively. As with grass consumption, the term $(1 + (ULWG_l/600) \cdot \mu \cdot GM(\rho_i)/2)^{0.75}$ accounts for the effect of the increased gain of sheep metabolic weight due to mixed grazing, in accordance with the IPCC (2006). For consistency with previous equations, $\mu_{sheep} = \mu$ and $\mu_{cattle} = 0$.

S_i is expressed through Eq. A.11:

$$S_i = \frac{\mathrm{Stoch}}{\Delta} \cdot \sum_{n \in \{biomass, SOC\}} (C_{n,i} - C_{n,0}) \tag{A.11}$$

where $C_{n,i}$ and $C_{n,0}$ are the amount of carbon stored in $kg \cdot ha^{-1}$ in compartment n for md_i and the baseline scenario, respectively. These compartments are SOC and the merged aboveground and belowground biomass. Stoch is a coefficient transforming the amount of carbon into a CO_2 equivalent based on the mass of C and O elements. Δ is the period in years during which stocks are compared.

SOC was expressed based on a stock change factors φ, as per the IPCC tier 1 scheme (2006). We used the IPCC tier-1 'moderately degraded' factor ($\varphi = 0.95$) and associated it with the maximum stocking rate possible, assuming that a complete gradual exploitation over the grazing season would only moderately degrade vegetation. We then applied it on a normalized gradient of residual biomass, to modulate its effect, as expressed by Eq. A.12 (the last term of the equation roughly ranges from 0 to 1):

$$C_{SOC,i} = \mathrm{SOC_{ref}} \cdot \left[1 - (1 - \varphi) \cdot \left(\frac{\mathrm{PUB} - RAB_i}{\mathrm{PUB}}\right)\right] \tag{A.12}$$

where $\mathrm{SOC_{ref}}$ is the default amount of C in $kg \cdot ha^{-1}$ in the first 30 cm of topsoil (in accordance with IPCC (2006)).

The biomass compartment $C_{biomass,i}$ is expressed via a root-to-shoot ratio to estimate the belowground compartment as per IPCC tier-2 (2006) (Eq. A.13):

$$C_{biomass,i} = \sigma \cdot (1 + \mathrm{rts}) \cdot \left(\frac{\mathrm{PUB} + RAB_i}{2}\right) \tag{A.13}$$

where σ and rts are proportion of carbon in biomass and root-to-shoot ratio, respectively. The last term of the right-hand side of the equation represents the mean biomass over the season (mean of PUB and RAB_i) rather than only the residual biomass in order to account for whole-season dynamics. Note that $C_{biomass,i}$ underestimates pasture biomass, as the overall standing biomass is higher than PUB (Hulin et al., 2010). However, this underestimation is corrected by the comparative approach we used. Indeed the subtraction involved by Eq. A.11 only evaluates the difference between stocks, not the value itself. Finally, the baseline $C_{n,0}$ was obtained through Eqs. A.12 and A.13 by replacing RAB_i by 0 (the baseline assumes that livestock consume all exploitable biomass).

Parameterization

For a given animal species l, the livestock parameters $ULWG_l$ and H_l^{LU} were obtained using animal weights derived from the local INRAE experimental farm of Laqueuille (Massif Central) and technical livestock references (Inosys, 2018). They were calculated for a grazing season duration D of 180 days. C_{LU} was taken from Baumont et al. (2006), PUB was from (Hulin et al., 2010), μ_l from d'Alexis et al. (2014), Δ from Searchinger et al.

Table A1
Parameters used in the model.

Parameter	Parameter description	Value	Source
$ULWG_{cattle}$	Cattle weight growth per livestock unit	151 kg·LU^{-1}	Inosys (2018) and this study
$ULWG_{sheep}$	Sheep weight growth per livestock unit	129 kg·LU^{-1}	Inosys (2018) and this study
μ	Maximum sheep weight gain increase due to mixed-grazing	0.3 (unitless)	d'Alexis et al. (2014)
PUB	Potential usable biomass for livestock production	5,300 kg	Hulin et al. (2010)
C_{LU}	Grass consumption per day per livestock unit	13 kg·day^{-1}·LU^{-1}	Baumont et al. (2006)
P_{cattle}	Price of cattle per kg of body liveweight	2.75 €·kg^{-1}	www.web-agri.fr (accessed August 2020)
P_{sheep}	Price of sheep per kg of body liveweight	3.33 €·kg^{-1}	www.web-agri.fr (accessed August 2020)
η	Erosion prevention baseline value	49 €	Van der Ploeg and de Groot (2010)
τ	Price of 1 kg of CO_2	0.02815 €	www.ember-climate.org (accessed September 2020)
$e_{CH4\_enteric,\ cattle}$	Enteric CH_4 emissions per year per head of cattle	57 kg·$head^{-1}$	IPCC (2006)
$e_{CH4\_enteric,\ sheep}$	Enteric CH_4 emissions per year per head of sheep	8 kg·$head^{-1}$	IPCC (2006)
$e_{CH4\_manure,\ cattle}$	Manure CH_4 emissions per year per head of cattle	6 kg·$head^{-1}$	IPCC (2006)
$e_{CH4\_manure,\ sheep}$	Manure CH_4 emissions per year per head of sheep	0.19 kg·$head^{-1}$	IPCC (2006)
$e_{N2O\_manure,\ cattle}$	Manure N_2O emissions per year per head of cattle	1.65 kg·$head^{-1}$	IPCC (2006)
$e_{N2O\_manure,\ sheep}$	Manure N_2O emissions per year per head of sheep	0.20 kg·$head^{-1}$	IPCC (2006)
$eCO2_{CH4}$	CO_2 equivalent of CH_4	28 (unitless)	IPCC (2013)
$eCO2_{NO2}$	CO_2 equivalent of N_2O	265 (unitless)	IPCC (2013)
H^{LU}_{cattle}	Number of heads of cattle per livestock unit	1.27 head·LU^{-1}	Inosys (2018) and this study
H^{LU}_{sheep}	Number of heads of sheep per livestock unit	7.37 head·LU^{-1}	Inosys (2018) and this study
Stoch	Ratio CO_2/C ratio, in mass	44/12 (unitless)	www.chemicalelements.com (accessed May 2019)
Δ	Reference period for comparison of management scenarios	100 years	Searchinger et al. (2018)
σ	Carbon proportion in plant biomass	0.47 (unitless)	IPCC (2006)
rts	Root-to-shoot pasture vegetation ratio	4 (unitless)	IPCC (2006)
SOC_{ref}	Soil organic carbon (reference scenario)	80,000 kg.ha^{-1}	IPCC (2006)
φ	Factor of soil organic carbon degradation	0.95 (unitless)	IPCC (2006)

(2018), P_l from www.web-agri.fr (August 2020), and τ from www.ember-climate.org/carbon-price-viewer (September 2020). SOC_{ref}, $e_{m,l}$, $eCO2_m$, δ, σ, φ and rts were obtained from IPCC (2006). η was calculated by averaging the monetary values of the erosion prevention service in grasslands in comparable Western countries from the database of Van der Ploeg and de Groot (2010). Stoch was calculated from the CO_2 chemical composition and the element masses obtained from www.chemicalelements.com (accessed May 2019). Table A.1 summarizes the values of the parameters used in the model.

Maximum animal density tested

As mentioned in Materials and Methods, we simulated animal densities between 0.1 and 2.26 LU·ha^{-1}. This 2.26 LU·ha^{-1} value is the maximum possible density as dictated by PUB ($PUB/(D \cdot C_{LU})$). This value is very close to 2 LU·ha^{-1} (1 LU·ha^{-1} annualized), which is close to the usual stocking rate in the area (Benoit and Lherm, 2018; Veysset et al., 2014). In our simulations, we eliminated the configurations where RAB_i was negative, which happened for the highest densities with balanced ratios. We thus remained within the limits we had fixed to our model, to avoid configurations where decreased grass availability would have impacted animal growth.

Appendix B:. Analysis of sensitivity to changes in ecosystem service values.

Table B.1.
Figs. B1 and B2.

Table B.1
Sensitivity analysis parameters.

Type of analysis	Parameter	Range of price scenarios in €. Letters in brackets refer to Fig. A.1 and A.2	Range of robustness of the PPF bundles (value in the model: 3.23)	Range of improvement of PPF bundle monetary value (value in the model: 10.59%)	Parameter range justification
One-at-a-time change of ES values	kg of CO_2 (τ)	0.00405 (a)–0.05225 (b)	2.63–3.52	10.60–11.67	Based on the price fluctuation range given by www.ember-climate.org (accessed Sept. 2020
	Erosion prevention (η)	32.56 (c) –88.00 (d)	3.40–3.00	11.35–09.74	Range of values given by Van der Ploeg and de Groot (2010)
	Beef(P_{cattle})	1.76 (e) –3.74 (f)	2.51–2.41	01.63–03.55	Based on the price fluctuation range given by Veysset et al. (2014)
	Mutton (P_{sheep})	2.13 (g)–4.53 (h)	3.23–4.53	00.79–03.18	Based on the price fluctuation range given by Veysset et al. (2014)
Simultaneous change in regulating and provisioning ES values	CO_2 & erosion prevention(τ and η)	See above:Low values (i) –Upper values (j)	2.60–3.21	10.86–09.32	See above
	Beef & Mutton (P_{cattle} and P_{sheep})	See above:Low values (k) –Upper values (l)	3.16–3.18	10.08–11.66	See above

*% of increase in monetary value of PPF bundles when transitioning from monospecific to mixed-grazing.

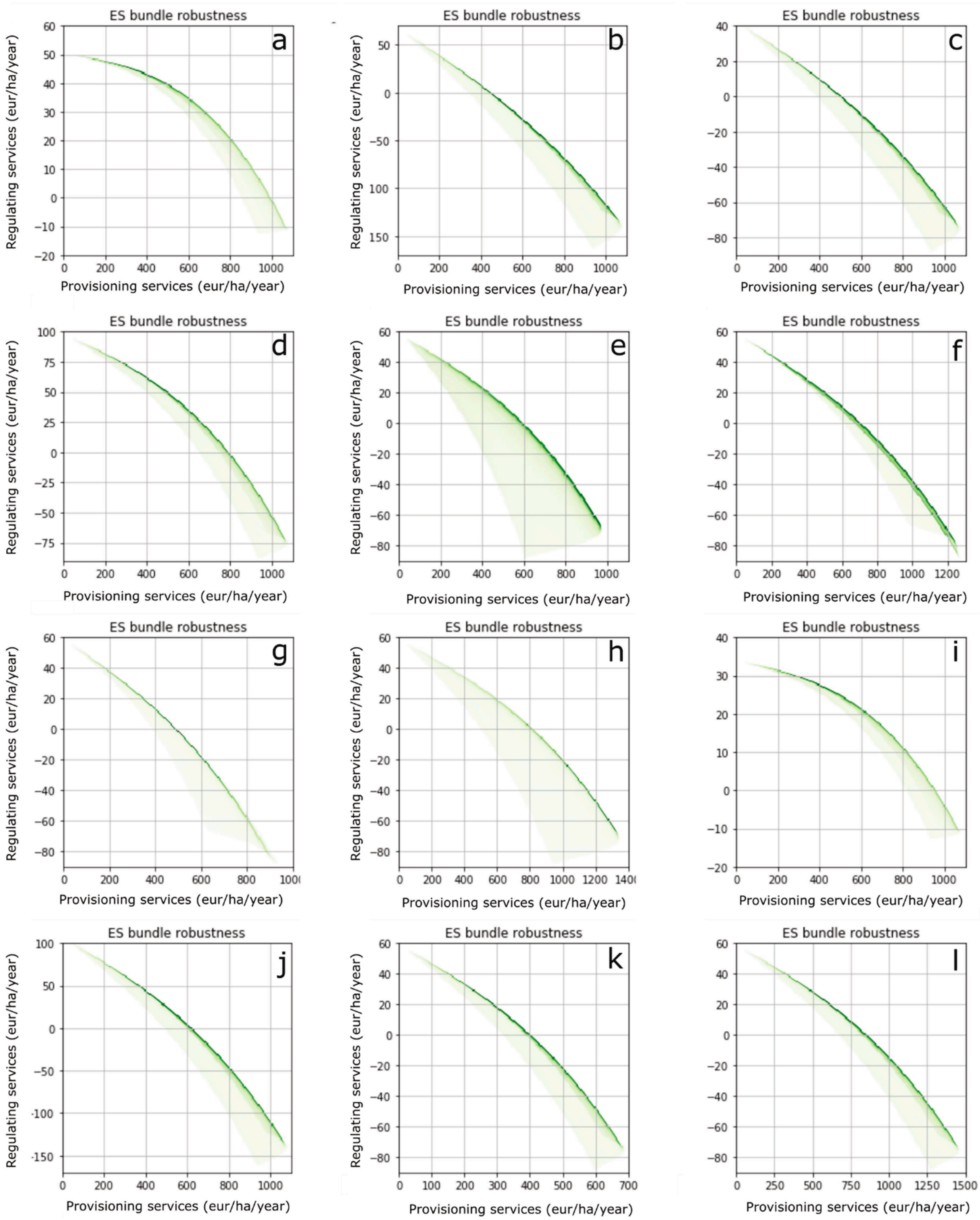

Fig. B1. Ensemble of ES bundles and their robustness. Letters refer to the price modifications in the sensitivity analysis listed in Table B.1.

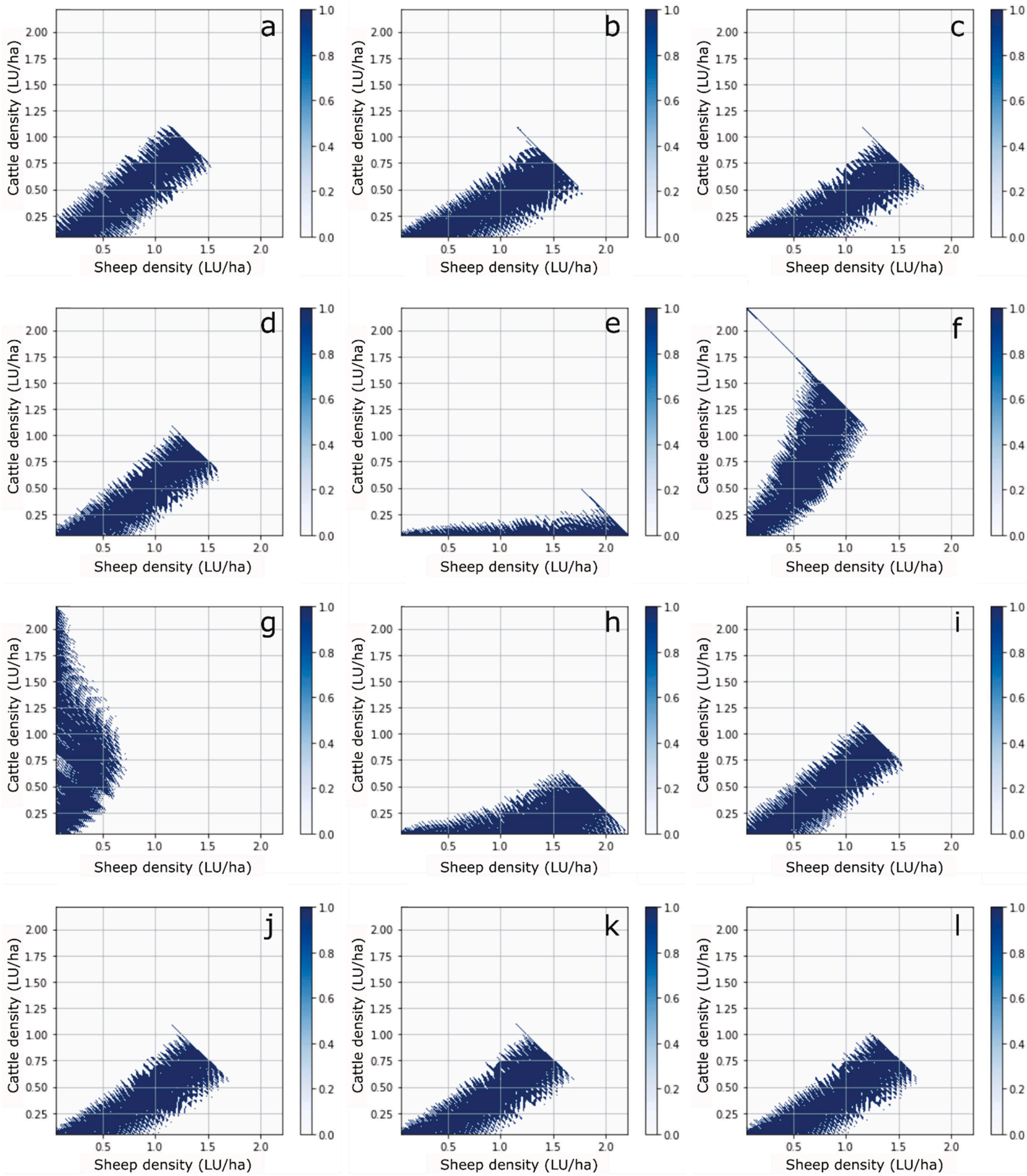

Fig. B2. Ensemble of management decisions providing PPF bundles. Letters refer to the price modifications in the sensitivity analysis listed in Table B.1.

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