Ecological Allee effects modulate optimal strategies for conservation in agricultural landscapes

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ABSTRACT

One target of biological conservation is the protection of biodiversity in agricultural landscapes. However, in their land-use decisions, farmers are often challenged with balancing biodiversity maintenance and profit generation. Under the current agricultural system, this tends to result in intensive farming which destroys suitable habitat for wild species. Thus, the potential for land-use conflicts between agriculture and biological conservation is high. Previous studies that investigated the effects of subsidies and taxes suggest mild trade-offs between conservation and farming, thus favouring land-sharing solutions to biological conservation. However, many ecological-economic models that dealt with this issue neglect possible Allee effects, which have been found by ecologists to be a common phenomenon. The existence of Allee effects markedly alters predictions of ecological-economic models: we show that conservation success is accompanied by substantial losses in agricultural production. More suitable habitat is required to prevent extinction of the species of interest, and conservation measures should start before the population has declined to some critical value. We emphasize the effect of spatial fragmentation on population viability under an Allee effect, as a clumped area of suitable habitat protects a population much better from extinction than a fragmented mosaic of habitat patches.

1. Introduction

An Allee effect describes a situation in which populations at low numbers or densities are affected by a positive relationship between population growth rate and density (e.g. Courchamp et al., 1999; Dennis, 1989; Lewis and Kareiva, 1993; Stephens et al., 1999). Higher population densities facilitate cooperation between individuals within a population or finding mating partners and, on the other hand, prevent imbreeding depression (Allen et al., 2005; Gascoigne et al., 2009; Gascoigne and Lipcius, 2004; Kramer et al., 2009; Kuussaari et al., 1998; McCormick, 2006). This positive density dependence can increase the extinction risk of a population if numbers are low. Although there is a lot of empirical evidence for Allee effects (e.g. Courchamp et al., 2000; Kuussaari et al., 1998; Lewis and Kareiva, 1993; Liebhold and Bascompte, 2003; Saccheri et al., 1998; Veit and Lewis, 1996) and they are assumed to be a common phenomenon (Kuussaari et al., 1998), they are often ignored in models for biological conservation. It is somehow paradoxical since the resulting higher extinction risk is of particular relevance to understanding threats to populations at low densities, which are typical targets of biological conservation (Berec,

2008; Courchamp et al., 1999; Dennis, 1989; Hanski, 1998; Lewis and Kareiva, 1993; Stephens and Sutherland, 1999; Stephens et al., 1999). Most simulations of population dynamics rely solely on negative density dependence, i.e., the per-capita growth rate declines as the population grows. A collection of dynamic models for populations in agricultural landscapes is given in Table 1. These models capture competition for food or nesting places well (Marshall et al., 2003). However, the reduced fitness for small population densities is not considered (Berec, 2011; Edelstein-Keshet, 1988). This raises the question of how robust the predictions of current models are to the inclusion of positive density dependence in growth processes.

In this paper, we show that to prevent extinction of a population with an Allee effect, conservation payments need to be much higher and start earlier than for the conservation of a population without an Allee effect. Our results can help to explain the decline of many species despite the existence of several agri-environment schemes; see, for instance, the "Farmland Bird Index" in the EU (Ramírez, 2018) or the report by the German Federal Ministry for the Environment, Nature Conservation and Nuclear Safety (Bundesministerium für Umwelt, Naturschutz und nukleare Sicherheit, 2020).

Table 1
Discrete-time dynamical models for populations in agricultural landscapes.

Model	Growth process	Dispersal in a spatially varying habitat	Modeled species	Positive density dependence possible
Hudgens and Haddad (2003)	Exponential, Quadratic	Yes	Not specified	No
Mildén et al. (2006)	Quadratic	Yes	Grassland plant	No
Sabatier et al. (2010); Tichit et al. (2007)	Beverton-Holt	No	Wader	No
Drechsler et al. (2007)	Hassell	Yes	Butterfly	No
Hartig and Drechsler (2009)	Indirect, Metapopulation	Yes	Not specified	No
Barraquand and Martinet (2011)	Ricker	Yes	Passerines	No
Sabatier et al. (2014)	Beverton-Holt	Yes	Lapwing	No
Mouysset et al. (2016)	Beverton-Holt, Ricker, Gompertz, Logistic	No	Several birds	No
This study	Ricker	Yes	Passerines	Yes

Not only the amount of suitable habitat, but also the spatial configuration can be important for the conservation success. An analogy can be made to *land sparing* and *land sharing.* Land sparing is typically defined as high-yielding agriculture on a small land footprint, whereas land sharing is typically defined as wildlife-friendly agriculture on a larger land footprint (Kremen, 2015). These definitions can be adapted slightly in the context of this paper, which focuses on mosaic landscapes in Europe's agricultural plains, where most of the land is farmed: instead of regarding land sharing as land which is simultaneously used for conservation and food production, we refer to it as a fine-grained mosaic of moderately and intensively used land patches, when the landscape is large compared to a single patch. Accordingly, we refer to spatially segregated areas of intensive crop production and extensive grasslands as land sparing.

Recent work by Fahrig (2017) and Sirami et al. (2019) provided empirical evidence for positive and negative ecological responses to land sharing according to this definition. Positive effects of land sharing were found under a variety of conditions, also in agricultural landscapes. In contrast, we show that land sparing solutions can have positive effects, namely by reducing the extinction risk for populations with Allee effects (Courchamp et al., 2008). A spatially aggregated population can save a subpopulation nearby that experiences a high risk of extinction. This phenomenon is known as a *rescue effect* (Brown and Kodric-Brown, 1977).

The remainder of this paper is organized as follows. In Section 2, a coupled ecological-economic model for agricultural land use is presented. We use the model of Barraquand and Martinet (2011) and modify the population dynamics by adding an Allee effect. Individuals are assumed to move between agricultural fields which are modeled on a grid. The economic part of the model follows Barraquand and Martinet (2011) and is therefore briefly described. In Section 3, we discuss trade-offs between conservation success and agricultural production in the presence of an Allee effect. We estimate conservation costs in different scenarios. Finally, we analyze the relevance of the spatial habitat configuration. In Section 4, we conclude and discuss the results.

2. Material and methods

2.1. Model framework

Farmland birds belong to one of the biological groups most threatened by habitat destruction and degradation due to intensive agriculture (Doxa et al., 2010). Birds are often used as umbrella or indicator species (Martikainen et al., 1998; Rubinoff, 2001; Suter et al., 2002) to indicate the biological state of a system, which has motivated many studies on birds in agricultural landscapes specifically (Table 1). Many bird species are very sensitive to agricultural land-use patterns in terms of finding nesting places or mating partners (Jiguet et al., 2000; Legendre et al., 1999), so that they could exhibit Allee effects. The following coupled ecological-economic model mimics the

metapopulation[1] dynamics of passerine birds in agricultural landscapes, as well as economic profits from agricultural land use. The model framework is adapted from Barraquand and Martinet (2011), and the majority of assumptions are kept identical. The population dynamics are modified to include an Allee effect. Changing only this part of the model of Barraquand and Martinet (2011) allows us to point out differences due to the Allee effect.

We consider a spatially explicit 10×10 lattice to simulate 100 fields of similar size and heterogeneous soil quality. Farmers are assumed to make profit-based land-use decisions. For simplicity, we consider two land-use types. Cropland use represents an intensive farming strategy, whereas grassland use stands for extensive, more ecologically friendly farming. As long as the soil quality in the field is sufficiently high, cropland use is the more profitable land use. The agri-environment scheme is designed in a way that subsidies are paid for grassland use to affect the land-use decision. The aim is to increase the grassland share to provide more suitable habitat for passerines. Note that spatial aggregation is not considered at first. For the ecological submodel, a stochastic metapopulation model is chosen to investigate how the species can adapt to local changes (e.g., Hodgson et al., 2009). An overview of the model structure with in- and outputs of the farmers' land-use decision is given in Fig. 1.

2.1.1. Modelling Allee effects

In many deterministic population models without overcompensation or Allee effects, the only stable steady state is the carrying capacity, which is reached for all initial conditions (except from zero). This situation can be seen in Fig. 2 (upper graph). Negative density dependence in the model due to competition for resources constrains population growth to a value K_2. In contrast, a strong Allee effect in a model produces bistability. That is, the positive density dependence at small numbers drives a population to extinction. Larger initial conditions lead to the respective carrying capacity K_1 as in models without Allee effect (Fig. 2, lower graph). The threshold A between persistence and extinction is called the (deterministic) *Allee threshold.* In the following, we are going to use a stochastic version of a population model with Allee effect. Stochastic population models have the property that all populations go extinct at some point due to random effects. Thus, we will use Monte-Carlo simulations to calculate the persistence probability for a time horizon of 100 time steps for given initial conditions.

2.1.2. Ecological model

The ecological component of the model consists of a metapopulation model for a single bird species in agricultural landscapes with the simplifying assumption of only two landscape types. Grassland is

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[1] We consider metapopulations to be collections of local populations that are linked by dispersal (Amarasekare, 1998; Barraquand and Martinet, 2011). Note that different definitions, particularly in classical metapopulation ecology, can be used.
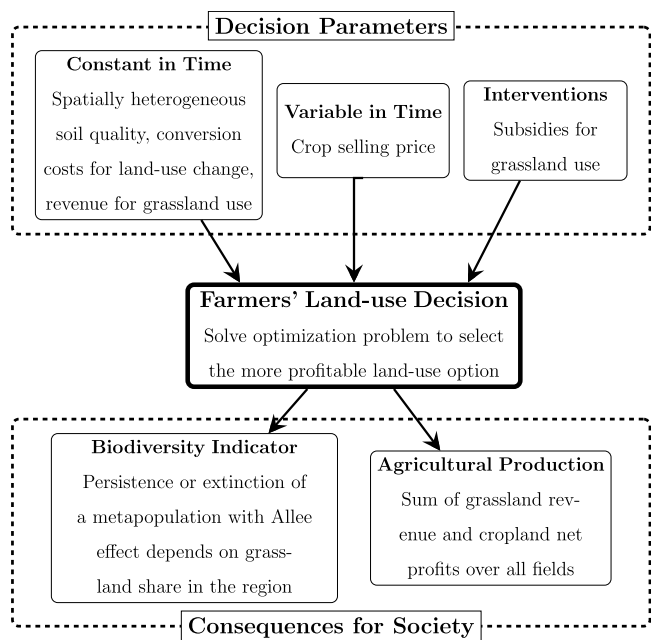
Fig. 1. Conceptual framework for the process of land-use decision. An optimization problem is solved to maximize the farmers' profit. The two outcome dimensions are affected by the decision.

assumed to provide suitable habitat for birds. In this case, we assume a Poisson-Ricker growth model with Allee effect

$$\mathbb{E}\left(N_{i,t_+}\right) = N_{i,t} \underbrace{e^{r_G\left(1 - \frac{N_{i,t}}{K}\right)}}_{F(N)} \underbrace{\frac{N_{i,t}}{\Phi + N_{i,t}}}_{G(N)} \, , \tag{1}$$

where $N_{i,t}$ is the local population size in patch i at time t, r_G is the intrinsic per-capita growth in grassland and K the carrying capacity. The time after reproduction and before dispersal is denoted by t_+. The Ricker model generates negative density dependence. That is, the growth function $F(N)$ decreases monotonically. By contrast, the term for Allee effect $G(N)$ includes positive density dependence, which is particularly important for small population sizes. The larger the value for Φ (in the following called Allee parameter), the stronger the positive density dependence in small populations. Function $G(N)$ is typically chosen for mate finding Allee effects (Courchamp et al., 2008). However, the model is rather phenomenological and the results do not depend on the choice of G.

Cropland, on the other hand, is detrimental for birds to persist. In this case, per-capita growth r_C is negative and density dependence is negligible. Then, the model equation reduces to:

$$\mathbb{E}\left(N_{i,t_+}\right) = N_{i,t} e^{r_C}. \tag{2}$$

In each time step, local population growth is followed by dispersal between the patches to connect the metapopulation. Dispersal is assumed to follow passive diffusion (for detailed information, see Appendix A). Parameter values of the ecological model are provided in Appendix C.

2.1.3. Economic model

The economic submodel consists of an optimization problem. Farmers are assumed to be rational and maximize profits. The annual gross return for grassland is given by the constant term

$$\pi_G = p_G + s_G, \tag{3}$$

where p_G is the revenue of grassland [€/ha]. The amount of subsidies for extensive grassland is denoted by s_G [€/ha]. The annual gross return for cropland is given by the function
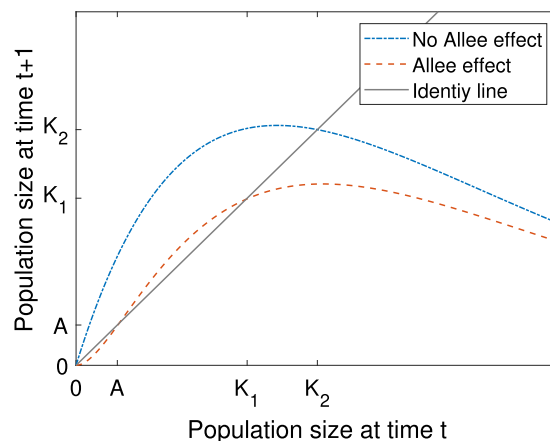

Fig. 2. Population size at time $t + 1$ as a function of population size at time t. Reproduction modeled by a deterministic version of Equation (1) without Allee effect ($\Phi = 0$; blue dash-dotted curve) and with Allee effect ($\Phi > 0$; orange dashed curve). The gray solid (identity) line denotes the case where the population size at time $t + 1$ equals the population size at time t. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$$\pi_C(p_C, Q, f) = p_C Y(Q, f) - \omega f - \nu_c, \tag{4}$$

where p_C [€/t] is the crop selling price, which varies over time. $Y(Q, f)$ [t/ha] is the crop yield, given by a Mitscherlich-Baule yield function. It depends on the agricultural intensity f for fertilizer and pesticide use and the beta distributed soil quality $Q \sim \beta(1.15, 2.05)$. Q is normalized in the range $[0, 1]$. It represents an index of the potential yield of the field (i.e., the maximal yield that could be obtained when no other input is limiting). Parameter ω [€/ha] describes the input cost [€/ha] and ν_c [€/ha] the fixed costs of cropland. For all details and parameter values, see Appendix B and Appendix C, respectively.

Farmers choose the land use in the next year by optimizing the expected net present value for a given time horizon H:

$$\max \sum_{t=t_0}^{t_0+H} \frac{1}{(1+\delta)^{t-t_0}} \times (\pi_t - C_t).$$

δ is the discount rate and π_t is the expected gross return in year t according to Eqs. (3) and (4). Parameter C_t serves to include the assumption that a change from one land use to the other is accompanied by additional conversion costs.

2.2. Quantities of interest

2.2.1. Production Possibility Frontier

When producing two outputs A and B with limited and partially shared inputs, producing more of output A means producing less of output B (Endres and Radke, 2012). All combinations of efficient production of outputs A and B can be visualized in a *Production Possibility Frontier* (PPF) (Nicholson and Snyder, 2012), showing the shape of the trade-off between production of A and production of B.

We will use a PPF to visualize consequences of farmers' land-use decisions. These are given by the persistence probability of passerines and the agricultural production[2] in the landscape. In most of the patches, the decision for cropland increases the agricultural production and decreases the persistence probability and the decision for grassland vice versa. However, due to heterogeneous soil qualities and variable crop prices, the trade-off between the persistence probability and agricultural production is not linear. The slope of the PPF gives

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[2] Sum over all fields of discounted actual profits (grassland revenue excluding subsidies plus cropland net profit) (Barraquand and Martinet, 2011).
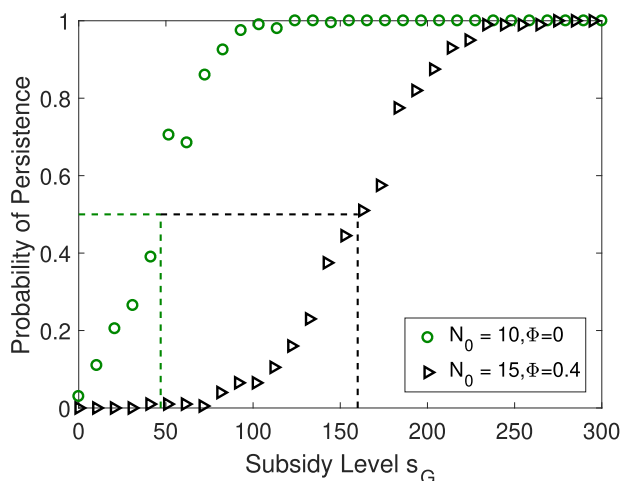
Fig. 3. Persistence probability as a function of the subsidy level s_G. Green circles: Initial local population size $N_0 = 10$ and no Allee effect $\Phi = 0$; black triangles: $N_0 = 15$ and $\Phi = 0.4$. Dashed lines indicate the subsidy level required for 50% persistence probability.

information about the *opportunity cost* for increasing the persistence probability (Endres and Radke, 2012). That is, at a position on the PPF with a flat slope, the persistence probability can be increased for less foregone agricultural production than at positions where the PPF has a steep slope. Moreover, the level of the PPF gives information about the maximum possible agricultural output. We will perform the analysis under these two aspects: the slope and the level of the PPF.

2.2.2. 50% persistence probability

Before biological conservation actions can be implemented, some strategic planning is needed, which includes the explicit formulation of conservation targets. Since environmental agencies or policy makers have to deal with different kinds of uncertainties, probabilistic measures of success are useful. To this end, we estimate the level of subsidies that is required to achieve a persistence probability of 50%. In order to do that, we calculate the persistence probabilities for several values of s_G for a time horizon of 100 time steps and 200 replicates (see Fig. 3). Then, we fit a sigmoid curve to the data points and get the subsidy level required for 50% persistence probability. This is shown with dashed lines in Fig. 3.

2.3. Spatial arrangement

We investigate effects of the landscape structure by comparing two spatial configurations of the soil quality Q. The values are generated by the same beta distribution in both cases. This allows us to investigate effects of habitat aggregation without changing the total amount of

habitat. The reference case is a spatially uncorrelated soil quality like in Fig. 4a. As explained above, we refer to this situation as land sharing. A spatial correlation is generated by a Gaussian random field $G(x, y)$ for all spatial coordinates (x, y) (using "Random Field Simulation" for MATLAB; see https://de.mathworks.com/matlabcentral/fileexchange/27613-random-field-simulation). To keep the exact same marginal beta distribution but with a spatial correlation, the generated values for Q are ranked, and then distributed at locations (x, y) so that $\text{rank}(Q(x, y)) = \text{rank}(G(x, y))$. This spatial arrangement results in land sparing and can be seen in Fig. 4b.

3. Results

3.1. Variation of Allee parameter Φ

The PPF-analysis without an Allee effect ($\Phi = 0$) indicates a weak trade-off between persistence probability and the agricultural production (see Fig. 5a, solid line, or Barraquand and Martinet (2011)). That is, the opportunity costs for improving the ecological outcome in the landscape are low. Fig. 5a shows additional results of simulations with an Allee effect for different values of Allee parameter Φ. By introducing the Allee effect, the trade-off between persistence probability and agricultural production becomes stronger. This means that, for stronger Allee effects, an improvement of the ecological outcome is accompanied by larger opportunity costs. For example, if the persistence probability should change from zero to one for $\Phi = 0.5$, the agricultural production would be reduced by a third.

The second observation of Fig. 5 is that the PPF is shifted downward with the Allee effect. An effective land-use strategy along the PPF is less productive than without an Allee effect. The color-coding of the plot shows why this is the case. A larger grassland share is required to achieve a certain persistence probability when the Allee effect is stronger. This implies less productivity.

3.2. Variation of the initial population size

Since Allee effects produce bistability in population models, the dependence on initial conditions is of particular interest. The PPF-analysis for an Allee parameter $\Phi = 0.4$ and several initial conditions is shown in Fig. 5b. For initial values far away from the deterministic Allee threshold ($A \approx 4.5$), no substantial difference is seen in the PPF (blue vs. black graph). If the initial population size gets closer to A, we observe a major trade-off between persistence probability and agricultural profit. The argument for the stronger trade-off is similar to the one discussed above: when the initial population size is sufficiently low, a large grassland share is required to reduce the risk of population extinction. There is a maximum of possible persistence probability which is smaller than one when $N_0 = 5$. That is, at some point, additional subsidies cannot increase the probability of persistence of the population. It shows that subsidies that start late (in the sense of populations having already declined to
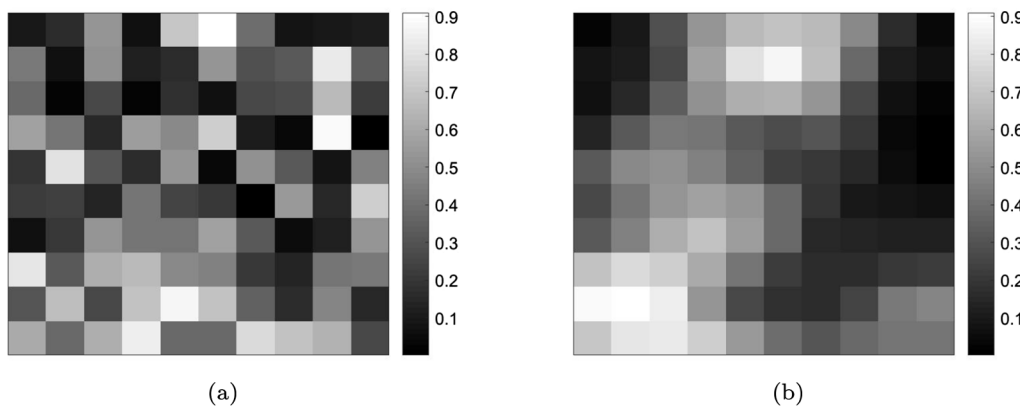

(a)

(b)

Fig. 4. Beta distributed soil quality Q in the landscape, spatially uncorrelated in (a) and arranged in a random field to obtain spatial clumping in (b). Q is normalized in the range [0, 1], which means that it represents an index of the potential yield of the agricultural field (i.e., the maximal yield that could be obtained when no other input is limiting) (Barraquand and Martinet, 2011). Note that soil qualities only differ in spatial arrangement, not in values.
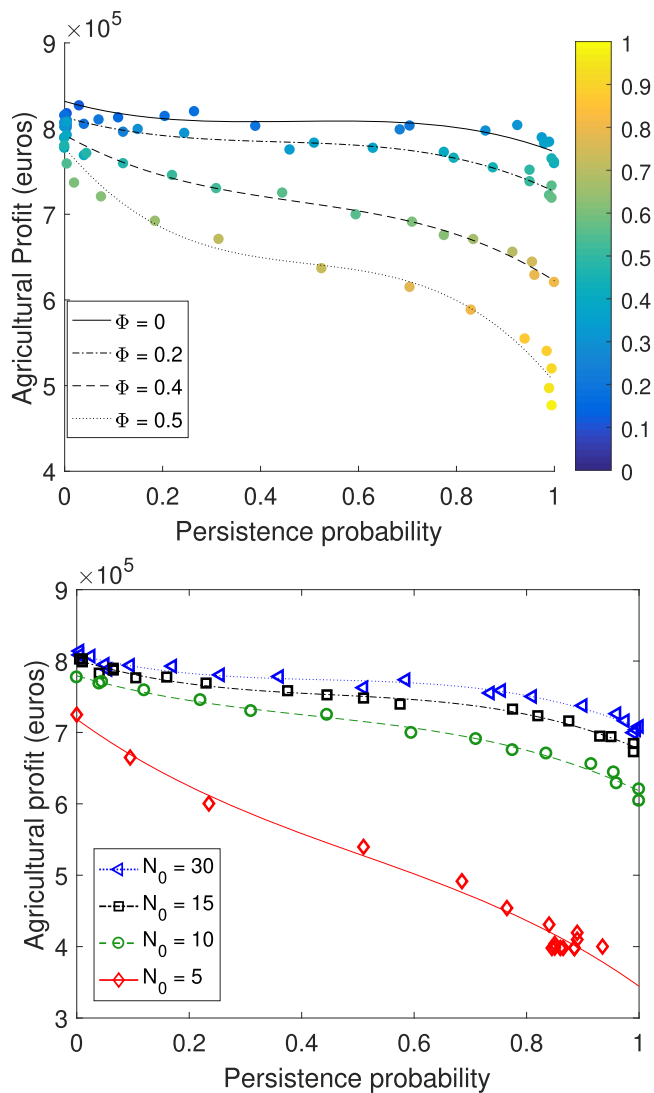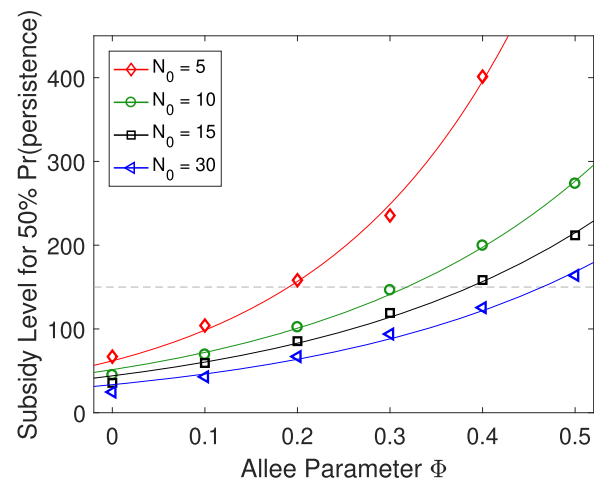
Fig. 6. Subsidy level that is required to achieve 50% persistence probability. Note that for $N_0 = 5$ and $\Phi = 0.5$ the conservation target cannot be achieved by any subsidy level; no data point exists. The dashed grey line indicates the mean subsidy level for extensive grassland in Germany in 2015 (Bundesministerium für Ernährung und Landwirtschaft, 2015).

in Germany at 2015 (Bundesministerium für Ernährung und Landwirtschaft, 2015). Note that it only serves to get an idea of existing payments: the model is not specifically parameterized for Germany.

Firstly, for larger initial populations less subsidies are required to achieve 50% persistence probability. This is seen by the vertical distance between points in Fig. 6. Without an Allee effect, the dependence on the initial population size is comparatively low. The stronger the Allee effect, the more the distance increases and thus the larger the dependence on initial conditions. Note that for the extreme case of $\Phi = 0.5$ and $N_0 = 5$ the conservation target cannot be achieved. The dependence on initial conditions shows that the conservation target can be achieved at lower costs when conservation actions starts earlier in time. Then, odds are higher that the population has not decreased to the regime of positive density dependence. When we compare simulation results for $\Phi > 0.2$ with the data from Germany (dashed line), we observe that the initial population size can be crucial for whether the conservation target of 50% persistence probability is achieved or not.

The second implication from Fig. 6 is that conservation costs progressively increase with the strength of the Allee effect. For a given initial population size, the subsidy level required for 50% persistence probability is an exponentially increasing function of Φ (see Fig. 6, fitted curves). If we consider the case of $N_0 = 5$, for instance, 50% persistence probability can be achieved with a subsidy level of $s_G \approx 100 \,[\text{€}/ha]$ when the Allee parameter is small ($\Phi = 0.1$). By contrast, s_G needs to be at a level of almost $250 \,[\text{€}/ha]$ when the Allee parameter is larger ($\Phi = 0.3$). The effects of Φ and N_0 are not additive but reinforce each other.

These results contain the following implications for conservation management: conservation success depends on initial conditions (also without Allee effects), due to stochasticity (Fahrig, 2017). However, an Allee effect can increase this outcome by about an order of magnitude and should rise awareness of the urgency of conservation actions. If conservation starts later in time, the species of interest may have declined to a small population value and enters the regime of positive density dependence. Then, it is much more costly or not possible to save it from extinction. The results for different values of Φ show that predictions about the costs of a conservation measure depend significantly on whether or not an Allee effect is taken into account.

3.4. Aggregation improves persistence probability

The spatial configuration of the landscape can play an important role for metapopulations with an Allee effect (Fahrig, 2017). To investigate this, we

Fig. 5. Production Possibility Frontier of the dynamic landscape for different values of the Allee parameter Φ (a) and different initial population sizes N_0 (b). The color bar in (a) indicates the mean grassland proportion in the landscape. Curves are polynomials of order 3 fitted by least squares method, ignoring values for persistence probability equal to 0 or 1. Monte-Carlo simulations with 200 runs. In (a), $N_0 = 10$. In (b), $\Phi = 0.4$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

small numbers) are less effective.

Fig. D.8 in Appendix D shows the corresponding PPF for the same set of initial conditions but without Allee effect ($\Phi = 0$). The different initial conditions lead to similar graphs which implies that demographic stochasticity can not serve as an explanation for the result in Fig. 5b. Thus, the big trade-off for $N_0 = 5$ must be due to the Allee effect.

3.3. Conservation target: 50% persistence probability

We now focus on conservation itself and which implications an Allee effect may have in terms of expected costs for policy makers or environmental agencies. Fig. 6 shows which amount of subsidies per field is required to achieve a persistence probability of 50%, when both initial conditions N_0 and the Allee parameter Φ are being varied. The dashed grey line shows the mean subsidy level for extensive grassland[3]

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[3] Requirements for the payment include to sacrifice nitrogen fertilizer use as well as the grassland renewal by reseeding.
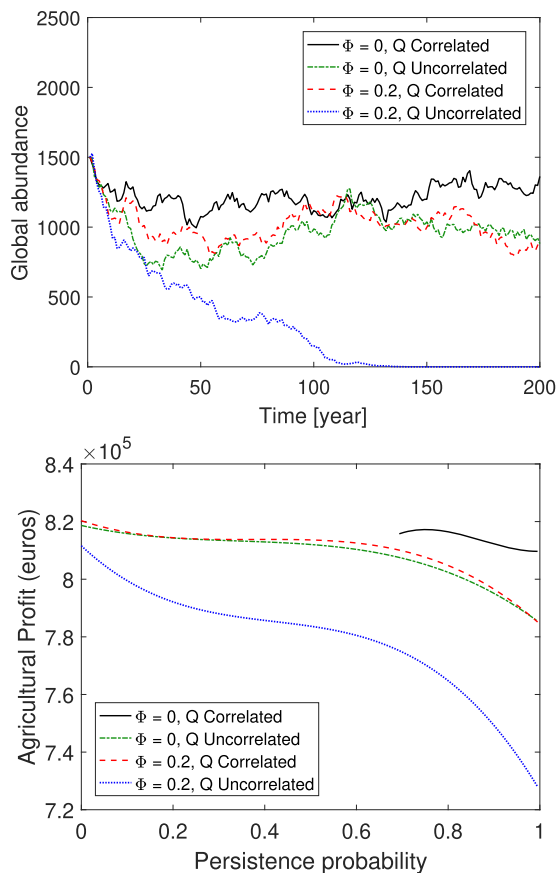
Fig. 7. Time series (a) and Production Possibility Frontier (b) of the dynamic landscape for $\Phi = 0$ and spatially correlated soil quality Q (black solid line), $\Phi = 0$ and spatially uncorrelated soil quality Q (green dot-dashed line), $\Phi = 0.2$ and spatially correlated soil quality Q (red dashed line) and $\Phi = 0.2$ and spatially uncorrelated soil quality Q (blue dotted line). $N_0 = 10$ in all four simulations. Initial land uses, crop price time series p_C and soil qualities in (a) are similar in all simulations to obtain comparable trajectories. Fitted curves in (b) are polynomials of order 3 fitted by the least squares method, ignoring values for persistence probability equal to 0 or 1. Data points are hidden for better clarity. Monte-Carlo simulations with 200 runs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

compare the results for a spatially uncorrelated soil quality Q with a spatially clumped configuration. The former represents a situation closer to land sharing whereas the latter is closer to land sparing. Fig. 7a shows time series of global population size for the cases with and without an Allee effect and the different spatial distributions of soil quality. The global abundance is higher when the soil quality Q is spatially correlated (plain black line versus green dot-dashed, and red dashed versus blue dotted line). This effect is much stronger in the case $\Phi = 0.2$. Furthermore, one can observe that negative outcomes due to the Allee effect can be compensated by the spatial aggregation of habitats (green dot-dashed versus red dashed lines).

These results hold also in the PPF (see Fig. 7b): The green dot-dashed curve shows again the PPF for the case without Allee effect ($\Phi = 0$) and uncorrelated soil quality Q. As previously discussed, with the introduction of an Allee effect the PPF is shifted downward and the slope is steeper. This is shown for $\Phi = 0.2$ by the blue curve. The spatial aggregation can counteract these changes. The red curve shows the PPF for the model Allee effect ($\Phi = 0.2$) and aggregated soil quality Q. It nearly matches the green curve without Allee effect and randomly arranged soil quality, as it was also seen in Fig. 7a. We suspect that the spatial aggregation of soil quality may induce a rescue effect, as the clumped habitat configuration can compensate negative outcomes due to the Allee effect. For the sake of completeness, the case without Allee effect ($\Phi = 0$) and correlated soil quality is given by the

black curve. Even without subsidies local populations survive in most of the simulations. The fitted curve begins at a persistence probability of 70%. However, the shift of the PPF due to aggregation is much smaller without Allee effect. This indicates a stronger effect of habitat aggregation in the presence of an Allee effect.

4. Discussion and conclusions

Many of the existing studies which investigate the impacts of conservation policies are using models for population dynamics with monotonic negative density dependence (Table 1). It is often useful to simplify in modeling (principle of parsimony), but the results presented here show that positive density dependence, when it is present and not taken into account, can lead to an overestimation of conservation success or, vice versa, an underestimation of conservation costs. This is in line with Kuussaari et al. (1998), who state that Allee effects complicate the task of conservation by increasing the likelihood of complex spatial dynamics and the risk of population extinction. Thus, understanding population dynamics in highly fragmented landscapes requires knowledge of both within-population phenomena such as Allee effects and relationships between several populations connected by dispersal.

We considered a coupled ecological-economic model for the conservation of a species with an Allee effect in an agricultural landscape. To account for both the conservation target and the task of food production of agriculture, we used a Production Possibility Frontier. We found a marked trade-off between conservation success and productivity in the landscape. The trade-off becomes stronger with a stronger Allee effect and for population numbers closer to the Allee threshold.

To estimate the expected costs of agri-environment schemes, we calculated the subsidy level s_G required to achieve a persistence probability of 50% over 100 years. It turned out that this subsidy level increases exponentially with the Allee parameter (Φ). Furthermore, the dependence on initial population sizes increases with Φ. The sensitivity to initial conditions shows that management is well advised to start as early as possible - this is always true of course, but it is particularly relevant in the presence of Allee effects, since bistability makes it very hard to recover once low population densities have been attained.

In additional simulations, we estimated also the total costs[4] instead of the subsidy level for 50% persistence probability. This value may be of interest to policy makers to estimate the required budget for a conservation measure. The results are not shown here, but are qualitatively the same as for persistence probability: total costs for conservation are higher to protect a species with than without an Allee effect. The larger the Allee parameter Φ, the higher the costs to achieve the conservation target. Again, the estimated total costs increase for a smaller initial population size.

Finally, we have shown the positive effect of spatially correlated soil quality on populations that suffer from positive density dependence at low population density. Natural or man-made aggregation of suitable habitat therefore enhances rescue effects from movement between patches and can help to prevent extinction of subpopulations (Hartig and Drechsler, 2009; Lewis and Plantinga, 2007). Thus, aggregation may reduce negative impacts of Allee effects (Kanarek et al., 2013; Kuussaari et al., 1998). The question of whether land sharing or land sparing strategies can meet the two objectives of food production and protection of biodiversity has been highly debated (Fahrig, 2017; Fischer et al., 2014; 2008; Kremen, 2015; Phalan et al., 2011). Some studies state that land sparing is a more promising strategy for minimizing negative impacts of food production (Phalan et al., 2011) while others argue that responses to land sharing were positive in a variety of conditions (Sirami et al., 2019). In this paper, we highlight that a conservation target that was typically believed to best achieved by land sharing – *sensu* a fine-grained mosaic of intensive and extensive habitats – might in fact benefit from strategies closer to land sparing (i.e., habitat aggregation,

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[4] Total costs are the accumulated subsidies over time and in the whole landscape.

localized protection measures) as one considers the potential Allee effects at work in many of these species dynamics. However, this result may hold only for short-distance dispersers, since an increased dispersal distance could also impede the rescue effect, as individuals disperse out of the favourable habitat cluster. To support clumped habitat areas, the concepts of agglomeration bonuses and spatial incentives were investigated (Drechsler et al., 2010; Parkhurst et al., 2002). When payments take a spatial component into account, the cost-effectiveness of a measure can be increased. We did not model spatially structured payments (man-made aggregation) but included similar effects by aggregating the soil quality to create clumped habitats (natural aggregation). Agglomeration bonuses could therefore be a solution for short-distance dispersers with an Allee effect.

In summary, we conclude that results from models for biological conservation that assume exclusively negative density dependent population growth do not entirely hold in the presence of an Allee effect. Our results show that the reduced population fitness due to an Allee effect leads to different conclusions compared to Barraquand and Martinet (2011), suggesting that classical habitat subsidies may not suffice to maintain persistence in many cases or will be much more costly. This may be part of the reason why some species cannot recover in spite of marked efforts to include favorable habitats in the landscape (Bretagnolle et al., 2018; Courchamp et al., 2000). In order to ascertain how to specify the population dynamics of species such as farmland birds in ecological-economic models, we suggest that it may be useful to generally pay more attention to population dynamic mechanisms leading to Allee effects - and to explicitly compile them in species lists and databases.

CRediT authorship contribution statement

Irina Vortkamp: Conceptualization, Methodology, Software, Formal analysis, Writing - original draft, Writing - review & editing. **Frédéric Barraquand:** Methodology, Software, Writing - review & editing. **Frank M. Hilker:** Conceptualization, Methodology, Writing - review & editing.

Declaration of Competing Interest

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Appendix A. Ecological Assumptions

A1. Dispersal

The dispersal process is given by

$$\mathbb{E}(N_{i,t+1}) = N_{i,t_+} + \sum_{j \neq i} \beta \frac{g(d_{ji})}{\sum_{k \neq i} g(d_{ki})} (N_{j,t_+} - N_{i,t_+}),$$

where $t + 1$ is the time after dispersal. β is the proportion of dispersing individuals in a field. g is a Gaussian dispersal kernel integrating to 1 with mean zero and standard deviation σ. This means many short-distance dispersers and few long-distance dispersers. d_{ji} is the distance between fields i and j which is calculated by the Euclidian distance. Periodic boundary conditions are chosen to prevent edge effects.

Appendix B. Economic Assumptions

B1. Price variability

The crop selling price at time t is given by

$$p_{C,t} - \bar{p} = B(p_{C,t-1} - \bar{p}) + u_t,$$

where B is a coefficient of autocorrelation, $p_{C,t-1}$ is the crop selling price in the previous time step, and u_t is a normally distributed random variable $u_t \sim N(0, 20)$. The crop selling price fluctuates around an average crop price $\bar{p}$ without an increasing or decreasing trend (see Deaton and Laroque, 1992, for details).

B2. Price expectations

Farmers are assumed to make rational price expectations given by

$$\mathbb{E}_{t-1}(p_{C,t+n}) = (1 - B^{n+1})\bar{p} + B^{n+1}(p_{C,t-1}).$$

B3. Agricultural yield

The achieved yield in a time step is given by the Mitscherlich-Baule yield function

$$Y(Q, f) = (Y_{inf} + Q(Y_{sup} - Y_{inf}))(1 - c_2 e^{-c_1 f}).$$

B4. Optimal input use f^*

We find the optimal input use by differentiating π_C with respect to t and solving $\frac{\partial \pi_C}{\partial f} = 0$:

$$f^*(p_C, Q) = -\frac{1}{c_1}\ln\left(\frac{\omega}{p_C c_1 c_2(Y_{inf} + Q(Y_{sup} - Y_{inf}))}\right).$$

Appendix C. Parameter values

The economic parameters are chosen following Barraquand and Martinet (2011). They are listed in Table C.2.

As in Barraquand and Martinet (2011) biological parameters are chosen for passerine birds which are an indicator of biodiversity in agricultural landscapes (Donald et al., 2001). They are listed in Table C.3.

Table C1
Parameter values for the economic model.

Name	Symbol	Value
Grassland benefits	p_G	191 [€/ha]
Mean crop selling price	$\bar{p}$	113.42 [€/t]
Fixed costs cropland	ν_c	222 [€/ha]
Input costs	ω	1.15 [€/kg]
Initial crop selling price	$p_C(t_0)$	220 [€/t]
Auto-correlation coefficient	B	0.559
Parameters for Mitscherlich response	c_1, c_2	0.015, 0.61
Minimum yield	Y_{inf}	4.8 [t/ha]
Maximum yield	Y_{sup}	10.8 [t/ha]
Conversion costs	$C_{C \rightarrow G}, C_{G \rightarrow C}$	200 [€], 50 [€]
Discount rate	δ	0.05
Time horizon	H	7 [year]

Table C2
Parameter values for the ecological model.

Name	Symbol	Value
Per-capita growth in croplands	r_C	− 0.1
Per-capita growth in grasslands	r_G	0.1
Carrying capacity	K	30 [Individuals]
Dispersal proportion per time	β	0.25
Dispersal range	σ	0.05
Initial population size (local)	N_0	$\frac{K}{3}$ [Individuals]

Appendix D

The PPF in Fig. D.8 without Allee effect ($\Phi = 0$) for several initial emphasizes that the results in Fig. 5b are not due to demographic stochasticity but due to the Allee effect.
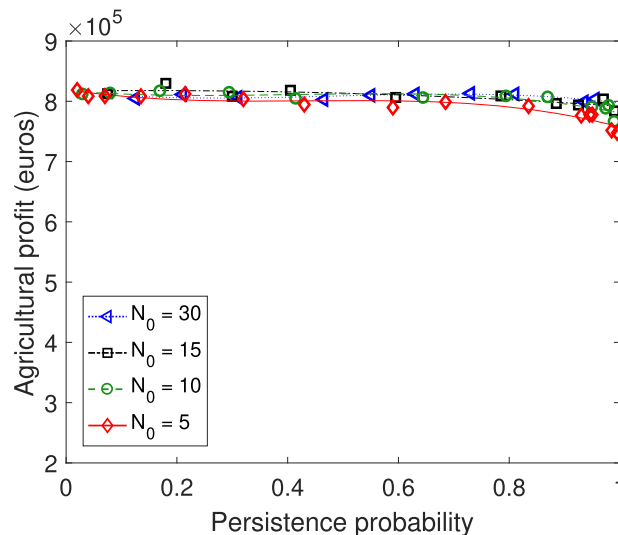

Fig. D1. Production Possibility Frontier of the dynamic landscape without Allee effect ($\Phi = 0$) for different initial population sizes N_0. Curves are polynomials of order 3 fitted by least squares method, ignoring values for persistence probability equal to 0 or 1. Monte-Carlo simulations with 200 runs.

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