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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

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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.

Keywords: Agri-environment schemes, Fragmented landscape, Production Possibility Frontier, Ecological-economic model

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. Dennis, 1989; Lewis and Kareiva, 1993; Courchamp et al., 1999; Stephens et al., 1999). Higher population densities facilitate cooperation between individuals within a population or finding mating partners and, on the other hand, prevent inbreeding depression (Kuussaari et al., 1998; Gascoigne and Lipcius, 2004; Allen et al., 2005; McCormick, 2006; Gascoigne et al., 2009; Kramer et al., 2009). 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. Lewis and Kareiva, 1993; Veit and Lewis, 1996; Kuussaari et al., 1998; Saccheri et al., 1998; Courchamp et al., 2000; Liebhold and Bascompte, 2003) 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 a higher extinction risk is of particular relevance to understanding threats

17 to populations at low densities which are targets of biological conservation
 18 (Dennis, 1989; Lewis and Kareiva, 1993; Hanski, 1998; Courchamp et al.,
 19 1999; Stephens and Sutherland, 1999; Stephens et al., 1999; Berec, 2008).
 20 Most simulations of population dynamics rely solely on negative density de-
 21 pendence, i.e., the per-capita growth rate declines as the population grows.
 22 A collection of dynamic models for populations in agricultural landscapes
 23 is given in Table 1. These models capture competition for food or nesting
 24 places well (Marshall et al., 2003). However, the reduced fitness for small
 25 population densities is not considered (Edelstein-Keshet, 1988; Berec, 2011).
 26 This raises the question of how robust the predictions of current models are
 27 to the inclusion of positive density dependence in growth processes.
 28 In this paper, we show that to prevent extinction of a population with an
 29 Allee effect, conservation payments need to be much higher and start earlier
 30 than for the conservation of a population without an Allee effect. Our results
 31 can help to explain the decline of many species despite the existence of sev-
 32 eral agri-environment schemes; see, for instance, the “Farmland Bird Index”
 33 in the EU (Ramírez, 2018) or the report by the German Federal Ministry
 34 for the Environment, Nature Conservation and Nuclear Safety (Bundesmin-
 35 isterium für Umwelt, Naturschutz und nukleare Sicherheit, 2020).
 36 Not only the amount of suitable habitat, but also the spatial configuration
 37 can be important for the conservation success. An analogy can be made to
 38 *land sparing* and *land sharing*. Land sparing is typically defined as high-
 39 yielding agriculture on a small land footprint, whereas land sharing is typi-
 40 cally defined as wildlife-friendly agriculture on a larger land footprint (Kre-
 41 men, 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 also 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

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
Tichit et al. (2007); Sabatier et al. (2010)	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

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.,

73 2010). Birds are often used as umbrella or indicator species (Martikainen
 74 et al., 1998; Rubinoff, 2001; Suter et al., 2002) to indicate the biological
 75 state of a system, which has motivated many studies on birds in agricultural
 76 landscapes specifically (Table 1). Many bird species are very sensitive to
 77 agricultural land-use patterns in terms of finding nesting places or mating
 78 partners (Legendre et al., 1999; Jiguet et al., 2000), so that they could exhibit
 79 Allee effects. The following coupled ecological-economic model mimics the
 80 metapopulation¹ dynamics of passerine birds in agricultural landscapes, as
 81 well as economic profits from agricultural land use. The model framework is
 82 adapted from Barraquand and Martinet (2011), and the majority of assump-
 83 tions are kept identical. The population dynamics are modified to include
 84 an Allee effect. Changing only this part of the model of Barraquand and
 85 Martinet (2011) allows us to point out differences due to the Allee effect.
 86 We consider a spatially explicit 10×10 lattice to simulate 100 fields of simi-
 87 lar size and heterogeneous soil quality. Farmers are assumed to make profit-
 88 based land-use decisions. For simplicity, we consider two land-use types.
 89 Cropland use represents an intensive farming strategy, whereas grassland
 90 use stands for extensive, more ecologically friendly farming. As long as the
 91 soil quality in the field is sufficiently high, cropland use is the more profitable
 92 land use. The agri-environment scheme is designed in a way that subsidies are
 93 paid for grassland use to affect the land-use decision. The aim is to increase
 94 the grassland share to provide more suitable habitat for passerines. Note

¹We 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, are used.

95 that spatial aggregation is not considered at first. For the ecological sub-
 96 model, a stochastic metapopulation model is chosen to investigate how the
 97 species can adapt to local changes (e.g., Hodgson et al., 2009). An overview
 98 of the model structure with in- and outputs of the farmers' land-use decision
 99 is given in Figure 1.

Figure 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.

100 2.1.1. Modelling Allee effects

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

116 2.1.2. Ecological model

117 The ecological component of the model consists of a metapopulation
 118 model for a single bird species in agricultural landscapes with the simplifying
 119 assumption of only two landscape types. Grassland is assumed to provide
 120 suitable habitat for birds. In this case, we assume a Poisson-Ricker growth
 121 model with Allee effect

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

Figure 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 .

122 where $N_{i,t}$ is the local population size in patch i at time t , r_G is the intrinsic
123 per-capita growth in grassland and K the carrying capacity. The time
124 after reproduction and before dispersal is denoted by t_+ . The Ricker model
125 generates negative density dependence. That is, the growth function $F(N)$
126 decreases monotonically. By contrast, the term for Allee effect $G(N)$ in-
127 cludes positive density dependence, which is particularly important for small
128 population sizes. The larger the value for Φ (in the following called Allee pa-
129 rameter), the stronger the positive density dependence in small populations.
130 Function $G(N)$ is typically chosen for mate finding Allee effects (Courchamp
131 et al., 2008). However, the model is rather phenomenological and the results
132 do not depend on the choice of G .
133 Cropland, on the other hand, is detrimental for birds to persist. In this case,

134 per-capita growth r_C is negative and density dependence is negligible. Then,
 135 the model equation reduces to:

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

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

140 2.1.3. *Economic model*

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

$$\pi_G = p_G + s_G , \quad (3)$$

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

$$\pi_C(p_C, Q, f) = p_C Y(Q, f) - \omega f - \nu_c , \quad (4)$$

147 where p_C [€/t] is the crop selling price, which varies over time. $Y(Q, f)$
 148 [t/ha] is the crop yield, given by a Mitscherlich-Baule yield function. It
 149 depends on the agricultural intensity f for fertilizer and pesticide use and
 150 the beta distributed soil quality $Q \sim \beta(1.15, 2.05)$. Q is normalized in the
 151 range $[0, 1]$. It represents an index of the potential yield of the field (i.e.,
 152 the maximal yield that could be obtained when no other input is limiting).

153 Parameter ω [€/ha] describes the input cost [€/ha] and ν_c [€/ha] the fixed
 154 costs of cropland. For all details and parameter values, see Appendix B and
 155 Appendix C, respectively.

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

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

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

162 2.2. Quantities of interest

163 2.2.1. Production Possibility Frontier

164 When producing two outputs A and B with limited and partially shared
 165 inputs, producing more of output A means producing less of output B (En-
 166 dres and Radke, 2012). All combinations of efficient production of outputs A
 167 and B can be visualized in a *Production Possibility Frontier* (PPF) (Nichol-
 168 son and Snyder, 2012), showing the shape of the trade-off between production
 169 of A and production of B.

170 We will use a PPF to visualize consequences of farmers' land-use decisions.
 171 These are given by the persistence probability of passerines and the agricul-
 172 tural production² in the landscape. In most of the patches, the decision for

²Sum over all fields of discounted actual profits (grassland revenue excluding subsidies plus cropland net profit) (Barraquand and Martinet, 2011).

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 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 Figure 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 Figure 3.

Figure 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.

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 Figure 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 dis-

tributed 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 Figure 4b.

Figure 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.

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 Figure 5a, solid line, or Barraquand and Martinet (2011)). That is, the opportunity costs for improving the ecological outcome in the landscape are low. Figure 5a shows additional results of simulations with an Allee effect for different values of Allee parameter Φ . By introducing the Allee effect,

Figure 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), $\Phi = 0.4$.

217 the trade-off between persistence probability and agricultural production be-
 218 comes stronger. This means that, for stronger Allee effects, an improvement
 219 of the ecological outcome is accompanied by larger opportunity costs. For
 220 example, if the persistence probability should change from zero to one for
 221 $\Phi = 0.5$, the agricultural production would be reduced by a third.
 222 The second observation of Figure 5 is that the PPF is shifted downward
 223 with the Allee effect. An effective land-use strategy along the PPF is less
 224 productive than without an Allee effect. The color-coding of the plot shows
 225 why this is the case. A larger grassland share is required to achieve a certain
 226 persistence probability when the Allee effect is stronger. This implies less
 227 productivity.

228 *3.2. Variation of the initial population size*

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

ready declined to small numbers) are less effective.
 Figure 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 Figure 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. Figure 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 grassland³ 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 Figure 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

³Requirements for the payment include to sacrifice nitrogen fertilizer use as well as the grassland renewal by reseeding.

264 target cannot be achieved. The dependence on initial conditions shows that
 265 the conservation target can be achieved at lower costs when conservation
 266 actions starts earlier in time. Then, odds are higher that the population
 267 has not decreased to the regime of positive density dependence. When we
 268 compare simulation results for $\Phi > 0.2$ with the data from Germany (dashed
 269 line), we observe that the initial population size can be crucial for whether
 270 the conservation target of 50% persistence probability is achieved or not.
 271 The second implication from Figure 6 is that conservation costs progressively
 272 increase with the strength of the Allee effect. For a given initial population
 273 size, the subsidy level required for 50% persistence probability is an expo-
 274 nentially increasing function of Φ (see Figure 6, fitted curves). If we consider
 275 the case of $N_0 = 5$, for instance, 50% persistence probability can be achieved
 276 with a subsidy level of $s_G \approx 100$ [€/ha] when the Allee parameter is small
 277 ($\Phi = 0.1$). By contrast, s_G needs to be at a level of almost 250 [€/ha] when
 278 the Allee parameter is larger ($\Phi = 0.3$). The effects of Φ and N_0 are not
 279 additive but reinforce each other.
 280 These results contain the following implications for conservation manage-
 281 ment: conservation success depends on initial conditions (also without Allee
 282 effects), due to stochasticity (Fahrig, 2017). However, an Allee effect can
 283 increase this outcome by about an order of magnitude and should rise aware-
 284 ness of the urgency of conservation actions. If conservation starts later in
 285 time, the species of interest may have declined to a small population value
 286 and enters the regime of positive density dependence. Then, it is much more
 287 costly or not possible to save it from extinction. The results for different
 288 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.

Figure 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. Dashed grey line indicates the mean subsidy level for extensive grassland in Germany in 2015 (Bundesministerium für Ernährung und Landwirtschaft, 2015).

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 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. Figure 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

300 green dot-dashed, and red dashed versus blue dotted line). This effect is
 301 much stronger in the case $\Phi = 0.2$. Furthermore, one can observe that
 302 negative outcomes due to the Allee effect can be compensated by the spatial
 303 aggregation of habitats (green dot-dashed versus red dashed lines).
 304 These results hold also in the PPF (see Figure 7b): The green dot-dashed
 305 curve shows again the PPF for the case without Allee effect ($\Phi = 0$) and
 306 uncorrelated soil quality Q . As previously discussed, with the introduction
 307 of an Allee effect the PPF is shifted downward and the slope is steeper.
 308 This is shown for $\Phi = 0.2$ by the blue curve. The spatial aggregation can
 309 counteract these changes. The red curve shows the PPF for the model Allee
 310 effect ($\Phi = 0.2$) and aggregated soil quality Q . It nearly matches the green
 311 curve without Allee effect and randomly arranged soil quality, as it was also
 312 seen in Figure 7a. We suspect that the spatial aggregation of soil quality may
 313 induce a rescue effect, as the clumped habitat configuration can compensate
 314 negative outcomes due to the Allee effect. For the sake of completeness, the
 315 case without Allee effect ($\Phi = 0$) and correlated soil quality is given by the
 316 black curve. Even without subsidies local populations survive in most of
 317 the simulations. The fitted curve begins at a persistence probability of 70%.
 318 However, the shift of the PPF due to aggregation is much smaller without
 319 Allee effect. This indicates a stronger effect of habitat aggregation in the
 320 presence of an Allee effect.

Figure 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.

321 4. Discussion and Conclusions

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

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

341 To estimate the expected costs of agri-environment schemes, we calculated
342 the subsidy level s_G required to achieve a persistence probability of 50% over
343 100 years. It turned out that this subsidy level increases exponentially with
344 the Allee parameter (Φ). Furthermore, the dependence on initial population
345 sizes increases with Φ . The sensitivity to initial conditions shows that man-

346 agement is well advised to start as early as possible - this is always true of
347 course, but it is particularly relevant in the presence of Allee effects, since
348 bistability makes it very hard to recover once low population densities have
349 been attained.

350 In additional simulations, we estimated also the total costs⁴ instead of the
351 subsidy level for 50% persistence probability. This value may be of interest
352 to policy makers to estimate the required budget for a conservation mea-
353 sure. The results are not shown here, but are qualitatively the same as for
354 persistence probability: total costs for conservation are higher to protect a
355 species with than without an Allee effect. The larger the Allee parameter Φ ,
356 the higher the costs to achieve the conservation target. Again, the estimated
357 total costs increase for a smaller initial population size.

358 Finally, we have shown the positive effect of spatially correlated soil quality
359 on populations that suffer from positive density dependence at low popula-
360 tion density. Natural or man-made aggregation of suitable habitat therefore
361 enhances rescue effects from movement between patches and can help to pre-
362 vent extinction of subpopulations (Lewis and Plantinga, 2007; Hartig and
363 Drechsler, 2009). Thus, aggregation may reduce negative impacts of Allee
364 effects (Kuussaari et al., 1998; Kanarek et al., 2013). The question of whether
365 land sharing or land sparing strategies can meet the two objectives of food
366 production and protection of biodiversity has been highly debated (Fischer
367 et al., 2008; Phalan et al., 2011; Fischer et al., 2014; Kremen, 2015; Fahrig,
368 2017). Some studies state that land sparing is a more promising strategy

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

369 for minimizing negative impacts of food production (Phalan et al., 2011)
370 while others argue that responses to land sharing were positive in a variety
371 of conditions (Sirami et al., 2019). In this paper, we highlight that a con-
372 servation target that was typically believed to best achieved by land sharing
373 – *sensu* a fine-grained mosaic of intensive and extensive habitats – might in
374 fact benefit from strategies closer to land sparing (i.e., habitat aggregation,
375 localized protection measures) as one considers the potential Allee effects
376 at work in many of these species dynamics. However, this result may hold
377 only for short-distance dispersers since an increased dispersal distance could
378 also impede the rescue effect, as individuals disperse out of the favourable
379 habitat cluster. To support clumped habitat areas, the concepts of agglom-
380 eration bonuses and spatial incentives were investigated (Parkhurst et al.,
381 2002; Drechsler et al., 2010). When payments take a spatial component into
382 account, the cost-effectiveness of a measure can be increased. We did not
383 model spatially structured payments (man-made aggregation) but included
384 similar effects by aggregating the soil quality to create clumped habitats
385 (natural aggregation). Agglomeration bonuses could therefore be a solution
386 for short-distance dispersers with an Allee effect.

387 In summary, we conclude that results from models for biological conserva-
388 tion that assume exclusively negative density dependent population growth
389 do not entirely hold in the presence of an Allee effect. Our results show
390 that the reduced population fitness due to an Allee effect leads to different
391 conclusions compared to Barraquand and Martinet (2011), suggesting that
392 classical habitat subsidies may not suffice to maintain persistence in many
393 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 (Courchamp et al., 2000; Bretagnolle et al., 2018). 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.

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Appendix A. Ecological Assumptions

Appendix A.1. 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.

412 Appendix B. Economic Assumptions

413 Appendix B.1. Price variability

The crop selling price at time t is given by

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

414 where B is a coefficient of autocorrelation, $p_{C,t-1}$ is the crop selling price
 415 in the previous time step, and u_t is a normally distributed random variable
 416 $u_t \sim N(0, 20)$. The crop selling price fluctuates around an average crop price
 417 $\bar{p}$ without an increasing or decreasing trend (see Deaton and Laroque, 1992,
 418 for details).

419 Appendix B.2. Price expectations

420 Farmers are assumed to make rational price expectations given by

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

421 Appendix B.3. Agricultural yield

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

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

424 Appendix B.4. Optimal input use f^*

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

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

427 **Appendix C. Parameter values**

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

Table C.2: 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]

429
 430 biological parameters are chosen for passerine birds which are an indicator of
 431 biodiversity in agricultural landscapes (Donald et al., 2001). They are listed
 432 in Table C.3.

Table C.3: 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]

433 Appendix D.

434 The PPF in Figure D.8 without Allee effect ($\Phi = 0$) for several initial
435 emphasizes that the results in Figure 5b are not due to demographic stochas-
436 ticity but due to the Allee effect.

Figure D.8: 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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