

BIOLOGICAL CONSERVATION:
MATHEMATICAL MODELS FROM AN
ECOLOGICAL AND SOCIO-ECONOMIC
SYSTEMS PERSPECTIVE

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“Art is a lie that helps us see the truth.”

— Pablo Picasso

“So it is with many simple beautiful models.”

— Joshua M. Epstein

Dedicated to the memory of my parents.

ABSTRACT

Conservation in the EU and all over the world aims at reducing biodiversity loss which has become a great issue in the last decades. However, despite existing efforts, Earth is assumed to face a sixth mass extinction. One major challenge for conservation is to reconcile the targets with conflicting interests, e.g. for food production in intensively used agricultural landscapes. Agriculture is an example of a coupled human-environment system that is approached in this thesis with the help of mathematical models from two directions.

Firstly, the ecological subsystem is considered to find processes relevant for the effect of habitat connectivity on population abundances. Modelling theory predicts that the species-specific growth parameters (intrinsic growth rate and carrying capacity) indicate whether dispersal has a positive or negative effect on the total population size at equilibrium (*r-K relationship*). We use laboratory experiments in combination with a system of ordinary differential equations and deliver the first empirical evidence for a negative effect of dispersal on the population size in line with this theory. The result is of particular relevance for the design of dispersal corridors or stepping stones which are meant to increase connectivity between habitats. These measures might not be effective for biological conservation.

A second population model, consisting of two coupled Ricker maps with a mate-finding Allee effect, is analyzed in order to examine the effect of bistability due to the Allee effect in combination with overcompensation in a spatial system. The interplay can cause complex population dynamics including multiple coexisting attractors, long transients and sudden population collapses. Essential extinction teaches us that not only small populations are prone to extinction but chaotic dynamics can drive a population extinct in a short period of time as well. By a comprehensive model analysis, we find that dispersal can prevent essential extinction of a population. In the context of conservation that is: habitat connectivity can promote rescue effects to save a population that exhibits an Allee effect. The two findings of the first part of this thesis have contrasting implications for conservation which shows that universal recommendations regarding habitat connectivity are impossible without knowledge of the specific system.

Secondly, a model for the socio-economic subsystem is presented. Agri-environment schemes (AES) are payments that compensate farmers for forgone profits on the condition that they improve the ecological state of the agricultural system. However, classical economic models that describe the cost-effectiveness of AES often do not take the social network of farmers into account. Numerical simulations of the socio-economic model presented in this thesis suggest that social norms can hinder farmers from scheme participation. Moreover, social norms lead to multistability in farmers' land-use decision behaviour. Informational campaigns potentially decrease the threshold towards more long-term scheme participation and might be a good tool to complement compensation payments if social norms affect land-use decisions.

Finally, a coupled human-environment system is analyzed. An integrated economic-ecological model is studied to investigate the cost-effectiveness of AES if the species of

concern exhibits an Allee effect. A numerical model analysis indicates large trade-offs between agricultural production and persistence probability. Moreover, conservation success strongly depends on the initial population size, meaning that conservation is well advised to start before the species is threatened. Spatial aggregation of habitat can promote rescue effects, suggesting land-sparing solutions for conservation. In that case, agglomeration bonuses may serve to increase the effectiveness of AES.

Possible causes for population declines are diverse and can be a combination of human influences, e.g. due to habitat degradation and inherent ecosystem properties. That complicates the task of conservation. The models presented in this thesis simplify complex systems in order to extract processes relevant for biological conservation. The analysis of spatial effects and dynamical model complexity, e.g. due to Allee effects or a nonlinear utility function, allows us improve the understanding of coupled human-environment systems.

PUBLICATIONS RESULTING FROM THIS THESIS

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INTRODUCTION

1.1 CONSERVATION - GENERAL INTRODUCTION

Biological conservation has a long history, and the view on nature and thereby the goals of conservation have transformed over time. Early conservation measures were concerned with the protection of ‘beneficial’ species and the regulation of ‘harmful’ species, while all others were ignored. A species was considered beneficial, for instance, if it controlled insects or weeds, whereas it was considered harmful when reducing yields. This *utilitarian* conservation approach regulated activities such as hunting, fishing and cultivating to obtain a continuous use of resources but was prone to unintended population declines of the neglected species (Weddell, 2002). Furthermore, population growth and rising standards of living in the twentieth century raised levels of resource consumption, habitat modifications and toxins in the environment. An accelerated loss of wild species heightened concern for species and habitats that do not provide commodities (Cardinale et al., 2012). However, this *preservationist conservation approach* was not to be reconciled with the needs of people who depended upon resources which created resentment and eroded support for conservation (Weddell, 2002). Thus, a combined approach that maintains biodiversity¹ and productive capacity was required to ensure human welfare and a sustainable life (IPBES, 2019; Weddell, 2002). The *suitable-ecosystem approach* focuses on the protection of ecosystem functions (e.g. food, clean water, biological control, nutrient cycling) rather than protecting single species or communities (Delacámara et al., 2020; Fryxell et al., 2014). But how can functioning ecosystems be best preserved?

The more species are present in a system, the greater is its resilience. Then, one single ecosystem function is provided by several species (redundancy) which enables the ecosystem to withstand perturbations (Fryxell et al., 2014). However, not all species make the same contribution to the ecosystem function (Shaffer, 1981). It is therefore important to identify *keystone species* that have a disproportionate effect on the persistence of all other species and play a pivotal role in the ecosystem functioning (Bond, 1994). A popular conservation approach is also the protection of *umbrella species* which require large expanses of habitat (Roberge and Angelstam, 2004). By protecting them, managers hope to protect habitat for many smaller, less-known species as well. This approach should be taken with caution, though, since indicators for protection are often derived from properties of charismatic species and do not account for the habitat requirements of species that contribute more to the ecosystem functioning (Roberge and Angelstam, 2004).

However, even if conservation has adapted to new conditions over time and much knowledge exists about the complexity of ecosystems, the rate at which species are going ex-

¹ The variety (richness, evenness, heterogeneity) of life at all levels of organization, including genetic material, species, communities and functional traits (Cardinale et al., 2012).

tinct is thought to have increased dramatically, indicating that a sixth mass extinction is under way (Barnosky et al., 2011; Ceballos et al., 2015; Mittermeier et al., 2011). The current threats on nature and biodiversity with the largest global impact are: habitat loss and modification, overexploitation, climate change, pollution and the introduction of novel pathogens, predators or competitors (e.g. Barnosky et al., 2011; Butchart et al., 2010; Maxwell et al., 2016; Rosser and Mainka, 2002; Steffan-Dewenter et al., 2007; Traveset and Richardson, 2006). Biodiversity loss will sooner or later lead to a loss of ecosystem services and thus feed back on human well-being (Cardinale et al., 2012; IPBES, 2019; Soliveres et al., 2016). Hence, conservation is an important task and research in biological conservation becomes increasingly relevant.

Mathematical models form an integral part of this research and have various areas of use. *Strategic* models can facilitate the understanding of the fundamental processes, most salient uncertainties, regions of robustness and important thresholds that determine population dynamics (Epstein, 2008; Fischer and Lindenmayer, 2007; Jopp et al., 2010; Schuwirth et al., 2019). *Tactic* models, in contrast, allow researchers to explore consequences of alternative policies and scenarios and inform managers about different strategies and practices (Cuddington et al., 2013; De Angelis et al., submitted; Francis and Hamm, 2011; Lester, 2019; Österblom et al., 2013; Schmolke et al., 2010).

Though much progress has been made in modelling ecological systems already, some relevant mechanisms remain obscure, some of which will be uncovered throughout this dissertation. Moreover, to do justice to conservation as an integrative process of protection of biodiversity and other human needs, mathematical models need to incorporate the ecological as well as the socio-economic component and identify feedbacks between the subsystems (Colding and Barthel, 2019). To this end, this thesis makes a contribution by the identification of pitfalls in biological conservation, if the complexity of one subsystem is underrepresented in the mathematical model. Let's do a little mind game to put the single components of this dissertation more into context. For the sake of simplicity, I confine the situation to conservation in terrestrial systems even if many issues are also relevant for aquatic systems.

1.2 POPULATIONS AT RISK OF EXTINCTION

Imagine you were a conservation manager and you had to develop a sound conservation policy. Which measures could you implement to protect a species of concern due to a low population abundance (Fischer and Lindenmayer, 2007; Shaffer, 1981)? Maybe the first thing one has in mind is to set aside a reserve. This will particularly help specialized species that need undisturbed or fragile habitat such as primary forests, swamps or tundra (Gibson et al., 2011; Kremen, 2015; Shaffer, 1981). Trophic interactions and other ecosystem-wide effects can be maintained. Thus, protected areas can simultaneously help large numbers of species and maintain whole ecosystems (Kremen, 2015). However, there are not many areas of natural or natural-like habitats left (Hanski, 2015) and a further increase in protected area would also accelerate land-use conflicts, e.g. with increasing demands for food (Kremen, 2015). Moreover, protected areas do not represent all ecosystems or communities (only around 50%) (Fryxell et al., 2014; Hayward, 2011; Weddell, 2002). Especially non-charismatic species such as microbes and

fungi are easily missed but important for the ecosystem functioning (Fryxell et al., 2014; Weddell, 2002). Thus, environmental conditions in human-dominated areas are nearly as important as those inside reserves (Laurance et al., 2012).

So, imagine that setting up a reserve would not be possible to protect the species of concern. Then, you had to identify factors that led to the small population abundance and figure out how they can be nullified (see Figure 1.1 for an overview). May interspecific interactions, such as competition, predation or missing food resources, be responsible for the decline (Blackburn et al., 2004)? One threat that has increased in the last decades due to globalization and human travel are pest or **invasive species** which damage ecosystems and harm biodiversity by outcompeting indigenous species, destruction of community interactions and change of the ecosystem functioning (Fei et al., 2019; Pyšek et al., 2020; Traveset and Richardson, 2006; Vilà et al., 2010). To date, it is not clear to which extent and under which circumstances invasion leads to extinctions directly (Gurevitch and Padilla, 2004). However, cascading effects may alter the community structure or destroy mutualistic interactions (Blackburn et al., 2004; Hanski, 2015). A positive example of what research in this field can achieve, is the push–pull technology² for pest control, which was found to have positive ecological, economic and social effects (Kremen, 2015). However, control measures should be evaluated before implementation. The introduction of predators as biological control agents went wrong many times in conservation history (Simberloff and Stiling, 1996).

Not only interactions with other species play a role but also **species-specific traits**, intraspecific interactions, group defense or complex breeding systems can affect the development of a population (Fischer and Lindenmayer, 2007; Hanski, 2015). As a conservation manager, it can be crucial to know about Allee effects³ which cause an increased risk for small populations to go extinct and are thought to have been responsible for the collapse of some populations already (Liermann and Hilborn, 1997; Myers et al., 1995; Stephens and Sutherland, 1999). All threats that are relevant for population declines may be more severe for species with Allee effects. Conservation attempts that artificially increase the population productivity (e.g. ex situ breeding, taking care for the survival of juveniles, supplemental feeding, artificial nest boxes (Weddell, 2002)) can then be particularly important since a minimum population size might be required for successful reproduction (Stephens and Sutherland, 1999). I fear that even if Allee effects are well-studied by ecologists, there is a lack of appropriate consideration in conservation.

Another possible threat for a species is **overexploitation**⁴. The challenge about this threat is quite obvious: conflicting ecological and economic interests can easily appear and make management particularly difficult (Weddell, 2002). Current conservation strategies to prevent overexploitation include the governance of sustainable harvest regimes and the enforcement of hunting regulations (Maxwell et al., 2016). To find a

2 The push–pull technology is a conservation agriculture approach based on a cropping system developed for integrated pest, weed and soil management in cereal–livestock farming systems. The pest insect is attracted to a trap plant (pull), and repelled from the main cereal crop using a repellent legume intercrop (push). Both companion plants provide high value animal fodder, facilitating milk production and diversifying farmers' income sources (Khan et al., 2011).

3 Positive density dependence at low population sizes (Stephens et al., 1999).

4 The harvesting of species from the wild at rates that cannot be compensated for by reproduction or re-growth.

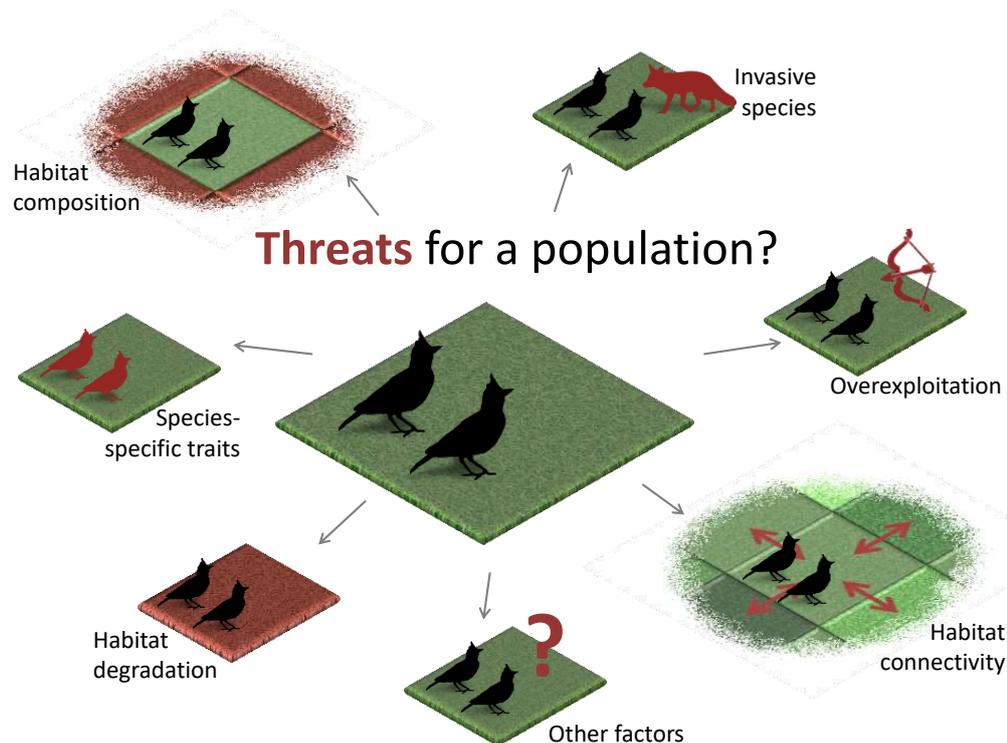


Figure 1.1: A species of concern and possible explanations for low population abundances. Note that it is intended to give a comprehensive outline of which aspects may affect population persistence. However, this can neither be complete nor unique.

balance between economic revenue, long-term yield and conservation, a lot of research is done on optimal control, adaptive-management and sustainable harvesting strategies (Hilker and Liz, 2020; Maxwell et al., 2016; Rosser and Mainka, 2002; Sugiarto et al., 2015).

Not only the species of concern can be exploited but the habitat in which it lives can contain resources that are used for economic purposes, e.g. for timber production (Gibson et al., 2011). **Habitat degradation** leads to missing food resources, breeding sites etc., which is why habitat loss is the greatest threat to biodiversity (Fischer and B. Lindenmayer, 2006; Fletcher et al., 2018; Hazell et al., 2004; Kerr and Deguise, 2004). One major problem about the effects of habitat loss is the time delay to biodiversity loss, called *extinction debt*, which makes problems prone to being underestimated (Brooks et al., 2002; Hanski, 2015; Litza and Diekmann, 2020; Tilman et al., 1994). Causes for habitat loss and degradation are wide-ranging and due to human population growth and accelerating demand for resources. Direct habitat loss occurs due to an expansion of agriculture, built areas and infrastructure (Fischer and Lindenmayer, 2007; Hanski, 2015; IPBES, 2019; Prescott et al., 2015), whereas indirect effects include logging, burning, waste disposal, recreation and effects of climate change (Cincotta et al., 2000; Pimm, 2008; Spooner et al., 2002). However, I want to distinguish between habitat modification and habitat loss since the effects can be quite different. Landscape modifications do not necessarily alter the numbers of species, but support a different species pool (Sabo et al., 2005) whereas habitat loss takes away any basis of existence. Habitat loss can be understood as a transformation of a natural landscape to anthro-

pogenic land cover, often called habitat matrix in conservation biology (Prescott et al., 2015). The impact of habitat loss on biodiversity is known for a long time as the *species-area relationship*, meaning that a smaller area of habitat can cover less species (Diamond, 1975). More research, however, is appreciated to understand how the quality of the habitat matrix can be improved to support species persistence (Driscoll et al., 2013).

Habitat modification, in contrast, can be seen as a moderate transformation, e.g. due to intensification of agriculture, but without a complete change of the biotope (Hanski, 2015). The challenge for conservation managers to protect species in this case is that conservation can not be implemented from scratch but needs to operate on private land (Weddell, 2002). Landowners generate their income e.g. by agriculture which can drastically shrink with a more environmentally friendly form of agriculture. The most common measure in the EU to solve that conflict of interest are *agri-environment schemes* (AES) to compensate farmers for forgone income who take land out of production or choose more extensive forms of agriculture in return (even if that is accompanied by lower food production, which can be another problem (Phalan et al., 2011a)). However, there is a lack of information of how effective these schemes are to maintain biodiversity (Kleijn and Sutherland, 2003). To that end, I study the cost-effectiveness of a grassland scheme in **Chapter 5**. It turns out that, all other things being equal, a situation which was previously assumed to provide sufficient amount of suitable habitat can lead to almost certain extinction for a species that exhibits an Allee effect. Hence, species that suffer from Allee effects need a greater amount of suitable habitats to persist which will cause higher conservation costs. A major challenge from the political point of view is that conservation is best to start before the population is threatened. However, the quantitative analysis given in this dissertation shows that conservation is more cost-effective if started immediately.

Another challenge for the success of AES is the voluntary basis. The design of schemes is often based on the simple economic assumption that farmers' seek to maximize profits. However, farmers' characteristics, tradition and previous experience of neighbouring farmers are important for participation in AES and their success as well (McCracken et al., 2015; Vanslebrouck et al., 2002). Quantitative approaches that address this gap between prediction and implementation are scarce. The socio-economic model in **Chapter 4** is a first attempt to include social norms in farmers' land-use decisions. The simulations reflect the hesitant participation of farmers in results-based schemes but indicate a great potential of informative campaigns to get stakeholders on board for long-term biological conservation. Successful wildlife-friendly management with no or few economic trade-offs can serve as good examples (Clough et al., 2011; Gordon et al., 2007; Prescott et al., 2015; Steffan-Dewenter et al., 2007).

Habitat loss often comes in tandem with habitat fragmentation since habitat loss might occur through subdivision of existing patches (Fahrig, 2003). Even though there is agreement about the negative effects of habitat loss on biodiversity, the question of which effect has fragmentation per se (independent of the effects of habitat amount) has sparked a recent debate. Fahrig (2017) collected studies in which biodiversity responses to fragmentation per se on a landscape scale were investigated with the surprising result that most significant effects of fragmentation were positive and many effects

were non-significant. Positive fragmentation effects on the landscape scale can result from reduced interspecific competition and predator escape over increased habitat diversity (increase in beta-diversity) and to a spread of risk (Fahrig et al., 2019; Fischer and Lindenmayer, 2007). The contrasting position states that metapopulation theory has clearly shown that effects of habitat fragmentation can increase extinction - and decrease colonization rates, leading to reduced likelihood of population persistence and lower diversity (Fletcher et al., 2018). Furthermore, mechanisms that are known to have variable effects such as edge effects or undesirable effects such as relaxation⁵ or isolation should not be neglected in answering the question of whether fragmentation has positive or negative effects (Fischer and Lindenmayer, 2007; Hanski, 2015; Renshaw, 1991; Traveset and Riera, 2005). Thus, there is no clear answer to the question of whether habitat fragmentation per se is good or bad for biodiversity which demonstrates how timely the topic is (Fahrig et al., 2019; Miller-Rushing et al., 2019). In practice, it may be useful to avoid fragmentation because fragmentation is almost always accompanied by habitat loss (Fletcher et al., 2018). However, the conclusions by Fahrig (2017) highlight that it is often a matter of spatial and temporal scale and one has to know the situation quite well to set up a successful conservation measure and evaluate it correctly (Hanski, 2015).

Even if I do not want to get into this debate of whether fragmentation per se has positive or negative effects in general, I will add two more factors that may be relevant: in **Chapter 3** I will, inter alia, analyze the effect of **habitat connectivity** on population dynamics of a species with overcompensation and an Allee effect and thereby uncover a new kind of rescue effect, called *DIPEE* – dispersal induced prevention of essential extinction. **Chapter 2** deals with the *r-K relationship*, a concept that was investigated recently but is not considered in the conservation literature so far (Arditi et al., 2015). It is based on the fact that habitats can differ with respect to the conditions for growth rates and for the carrying capacity. This dissertation provides the first experimental evidence for a negative r-K relationship, suggesting that connectivity between heterogeneous environments can be detrimental for the population abundance.

On the basis of these findings, I want to stress the idea of dispersal corridors to bridge the gaps between habitats, on which conservation biologists have focused a great deal of attention (Weddell, 2002). Even if habitat loss and fragmentation often go hand in hand, this may not necessarily hold for the reversal. Corridors can reduce fragmentation and not habitat loss. The effect for biological conservation is therefore doubtful (Fischer and Lindenmayer, 2007; Miller-Rushing et al., 2019). Conversely, maximizing the total amount of habitat conserved, irrespective of its level of fragmentation, will do no harm (Fahrig et al., 2019).

The interplay of habitat size, fragmentation and isolation leads me to the last point a conservation manager could investigate, namely the **habitat composition** or spatial arrangement of habitat. It is mostly dictated by other human interests for space, e.g. for agriculture, industry or residential development (Fryxell et al., 2014). However, attempts like agglomeration bonuses⁶ have recognized that the spatial configuration of habitat can be an important contribution for conservation by preventing movement of

5 decline in species richness, which occurs when populations become extinct because an island is too small to support viable populations (Weddell, 2002)

6 Agglomeration bonuses are an incentive in agriculture to cumulate wildlife-friendly farming areas.

Table 1.1: Threats on population persistence and the chapters in this thesis addressing these threats.

Threat	Chapter
Allee effect	Chapters 3, 5
Habitat quality	Chapters 4, 5
Habitat connectivity	Chapters 2, 3
Habitat composition	Chapter 5

individuals through the harmful habitat matrix (Drechsler et al., 2010; Parkhurst et al., 2002). In **Chapter 5**, I will close a research gap by investigating how much a species with an Allee effect could benefit from rescue effects due to an aggregation of habitat. The results are embedded in the land sharing vs land sparing debate⁷ to account also for the economic consequences of different strategies.

In the end, for the successful protection of a species of concern, a conservation manager will have to know many properties about the species as well as the system it lives in. The factors that trigger species' declines need to be clearly identified, reduced or reversed (Weddell, 2002). These dynamics between human behaviour and ecosystems express complex interaction and feedback processes (Jopp et al., 2010). Fortunately, mathematical modelling can facilitate insights into how organisms interact with the environment and each other, and how this creates the properties of ecological systems (Jopp et al., 2010). Models provide an opportunity to test hypotheses in a virtual laboratory and explore a whole manifold of numerically calculable scenarios (Epstein, 2008; Weidlich, 2006). The threats on population persistence explored in this thesis with the help of models are listed in Table 1.1. Investigation of spatial aspects of habitat fragmentation, quality, arrangement and the surrounding matrix in real ecosystems could be time-consuming and costly in the best case (Österblom et al., 2013; Velten, 2009). Ethical conflicts can arise due to irreversible interventions and the uniqueness of ecosystems often make empirical investigation impossible (Samarskii and Mikhailov, 2002; Velten, 2009). Then, mathematical models are the only tool to obtain a better understanding.

1.3 MATHEMATICAL MODELS IN SUPPORT OF INTERDISCIPLINARY PERSPECTIVES

Mathematical models can promote interdisciplinary dialogue and collaboration in different fields in two ways, both of which will be applied in this dissertation. On the one hand, the structural and dynamical similarities between mathematical models allow applications in different contexts and thus have large explanatory power (Helbing, 1995; Weidlich, 2006). Let me give one example: the famous Lotka-Volterra predator-prey

⁷ The debate addresses the question of whether land sparing - high-yielding agriculture on a small land footprint - or land sharing - low-yielding, wildlife-friendly agriculture on a larger land footprint - will promote better outcomes for local and global biodiversity (Kremen, 2015).

model in ecology produces oscillating dynamics with sequential cycles (e.g. Berryman, 1992). These also occur in economics - called business cycles between employment rate and wage share (Feinstein and Dobb, 1967). Thus, the Goodwin model in economics is mathematically similar to the Lotka-Volterra model, associating the employment rate with prey and the wage share with the predators.

The advantage of these structural similarities is that knowledge of one discipline can be easily transferred to other disciplines (Fryxell et al., 2014). I am going to use the genericity of mathematical models for the first part of this dissertation (**Chapters 2 and 3**). A few model assumptions are placed on the system, so that the model is neither species- nor site-specific. Therefore, the model probably holds for a variety of systems and allows to test for relevant processes. I make use of the generic model properties in the model validation in **Chapter 2**. In the lab, one can choose a model organism with short generation times to reduce experimental effort. The findings, however, permit conclusions for a range of species on the ecological scale since it is based on only a few assumptions (logistic growth in this case). Furthermore, the generic model as well as the experimental approach allow to control for a single process (Becks et al., 2005; Gokhale et al., 2018). However, one should have in mind that the (implicit) underlying assumptions do not always hold for another system. Similarities need to be investigated carefully before applying a model to another context.

The second opportunity mathematical modelling has for interdisciplinary work is the coupling of models originating from different disciplines (Proskurnikov and Tempo, 2017). Even if the need for interdisciplinary models to approach questions of conservation was recognized in the last years, one subsystem is often underrepresented (McKane et al., 2020). Understanding the intricate feedbacks between socio-economic and ecological systems, however, requires coupled models that account for the complexity and non-linearities of both components (Kremen, 2015; Steffan-Dewenter et al., 2007; Sun, 2019). This is of particular relevance if one subsystem is multistable and has tipping points at which the system can abruptly shift to another state (Bauch et al., 2016; Rocha et al., 2018; Sun and Hilker, 2020a; Suzuki and Iwasa, 2009). While much effort was made on regime shifts in ecological systems (e.g. Scheffer et al., 2009), the effects are less recognized for social systems (Biggs et al., 2018; Nyborg et al., 2016). The coupled socio-economic model in **Chapter 4** shows that social norms can serve to explain the reluctance to participation in AES by farmers despite compensation payments. Bistability due to social norms may inhibit the raise of participation levels initially. However, informative campaigns have the potential to induce a shift to a more desirable state in the long-term. Thus, the social model component feeds back on the economic submodel.

It is not trivial to combine modelling approaches from different fields and to unify them in an integrated dynamical system. To that end, I will next give a short overview about approaches to modelling spatio-temporal dynamics in different disciplines and how this dissertation is embedded in this variety of modelling techniques.

1.4 SPATIO-TEMPORAL DYNAMICS IN ECONOMIC, ECOLOGICAL AND SOCIAL SYSTEMS

This section serves to introduce some concepts used to describe relevant systems for this dissertation (ecological, economic, social) and to outline similarities and differences. One straightforward way to classify models is based on the mathematical technique used. Even if this tells little about the models' predictive or explanatory power (De Angelis et al., submitted), it may be helpful to get an intuition of which questions are addressed by which methods, how these are combined and which problems can appear by coupling. Moreover, the model formulation is relevant since apparently the same model can give different answers, depending on whether a particular variable is discrete or continuous (Durrett and Levin, 1994; Turchin, 1998). A summary of models that differ in considering time, space and state variables in continuous versus discrete units, is listed in Table 1.2. Note that not all types of models listed in the table will be specified in the following but a selection will be mentioned to delimit the methods used throughout this dissertation.

Table 1.2: Categorization of spatio-temporal models after Caswell and Etter (1993) and Turchin (1998). State variable can be continuous (blue) or discrete (red), respectively.

		Time	
		Continuous	Discrete
Space	Continuous	Partial differential equations Integro-differential equations	Integrodifference equations Individual-/agent-based models
	Discrete	Reaction-diffusion networks Set of ordinary differential equations Interacting particle systems	Coupled map lattices Cellular automata Individual-/agent-based models

1.4.1 State variables

Different disciplines are unique in the questions that they address, the key state variables used and the quantification of those. Economic models mostly deal with some form of capital as the state variable with a natural order – the more the better. Questions that are typically addressed in economics deal with maximization of outputs or minimization of costs, in short: optimization problems (Nicholson and Snyder, 2012). The mathematical methods used for the analysis differ in the kind of algorithm but all deal with some kind of objective function that is to be optimized. The mind set in social sciences is somehow the opposite in this respect. Quantifiable units are hardly reasonable to describe culture, tradition or information and therefore no clear objective can be stated. This is maybe why mathematics are used less to describe social systems (Malchow, personal communication). Social theories based on mathematics is probably most known in social network analysis (Bonacich and Lu, 2012; Helbing, 1995). Ecological systems are somehow in between. State variables such as numbers of individuals or biomass can be quantified but there is no inherent value - the population abundance of a native species

is treated differently than the abundance of an invasive species.

One possibility to put all disciplines on the same page is to assign a monetary value to all state variables. It is done, for instance, to value ecosystem services (Hein et al., 2006) but also to rank desirability of different situations in economics (Nicholson and Snyder, 2012). In the latter case, the exact value of *utility* is meaningless. However, it can be useful to incorporate non-monetary decision parameters in quantitative models. This will be discussed further in **Chapter 4**.

A classification of state variables that is borrowed from fluid dynamics distinguishes between *Eulerian* and *Lagrangian* perspective, respectively. In ecological contexts, the Lagrangian description is centered on the (moving) individual (Turchin, 1998). It can be used to understand home ranges, the ecological niche of a species or trait variation. The Eulerian description, in contrast, focuses on population densities as the state variable. It is used in this dissertation to understand spatio-temporal population dynamics but is also useful for many biodiversity-related questions, such as understanding whole species communities or food web modules including predator-prey, mutualistic or competitive interactions. In mathematical sociology, the Lagrangian description is used to investigate the evolution of opinions, considerations, decisions and actions of individual social actors (Mirtabatabaei et al., 2014; Proskurnikov and Tempo, 2017; Weidlich, 2006). This approach will be used in **Chapter 4** to account for how farmers' in a social network influence each others' behaviour. The Eulerian description, in contrast, focuses on the changes of relevant collective macrovariables on a larger scale such as society culture, political conviction or religion (Proskurnikov and Tempo, 2017; Weidlich, 2006).

Modelling techniques differ with respect to the kind of approach used. Agent-based models (ABMs) in sociology and economics, or individual-based models (IBMs) in ecology cover the Lagrangian point of view (Schweitzer, 2003). These models are employed at smaller spatio-temporal scales and observe every individual or agent in its temporal development (Canuto et al., 2012). IBMs and ABMs are popular for practitioners because they can be connected to specific empirical systems (De Angelis et al., submitted). A disadvantage however is that little general theoretical progress can be made with models containing detailed description of one system (Railsback and Grimm, 2019). Furthermore, documentation and reimplementing is challenging and parameterization requires a large amount of data (De Angelis et al., submitted).

In contrast, Eulerian models that distill key processes are used to model the spatio-temporal dynamics of the system at a larger scale (Turchin, 1998). This model type, usually formalized in differential or difference equations, is based on a large theory and has the opportunity for rigorous mathematical proofs. Therefore, Eulerian models can have large explanatory power and provide fundamental concepts. A majority of the underlying processes that can harm a population (Section 1.2) are typically represented by Eulerian models. Finally, it depends on the model objective whether a general, strategic model or a precise, tactic model is chosen (Holling, 1966).

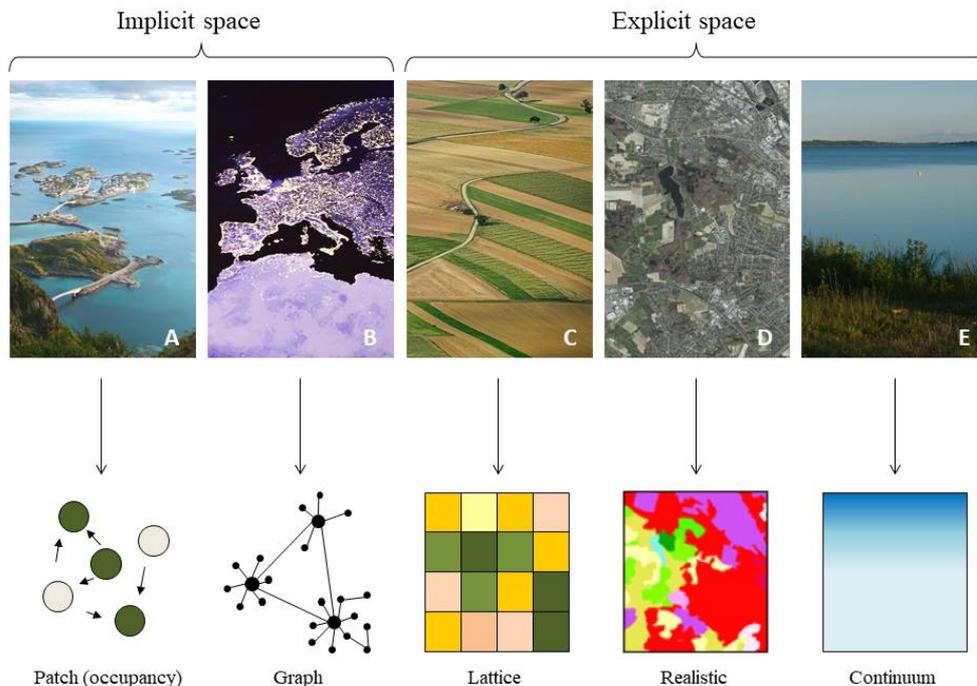


Figure 1.2: Different levels/purposes of simplification in spatial models. Sources of maps in D: OpenStreetMap and Umweltbundesamt, Germany.

1.4.2 Spatial dimension

Spatial aspects in a model can spawn emergent properties of a system that can not be studied with a mean field approach (Schweitzer, 2003). The great variety of plankton species in lakes, for instance, can be explained with the help of a spatial model. The corresponding local model fails at the *principle of competitive exclusion*⁸ (Atkinson and Shorrocks, 1981; Durrett and Levin, 1994; Levin, 1974; Tilman, 1994). However, mathematical models vary in the level of abstraction, depending on the scope of the study, the resolution and realism (see Figure 1.2 for an overview) (Durrett and Levin, 1994). Models with an implicit spatial dimension have a high degree of abstraction. *Patch (occupancy) models* (Figure 1.2A) only record the fraction of occupied patches, irrespective of the spatial arrangement and differences between patches (Caswell and Etter, 1993; Durrett and Levin, 1994; Hanski and Simberloff, 1997). The theory in population ecology goes back to Levins (1969) who described classical metapopulations as a collection of patches in a dynamic equilibrium of extinctions and recolonizations (Hanski and Gilpin, 1991). The model was modified to study rescue effects, habitat loss, spatial heterogeneity (mainland-island or source-sink systems) and builds the cornerstone of spatially distributed population models with numerous ecological examples (Brown and Kodric-Brown, 1977; Fryxell et al., 2014; Hanski and Gilpin, 1991). A sec-

⁸ The principle of competitive exclusion suggests that, in homogeneous environments, species that compete for the same resource cannot coexist, so that one species should win over the other. That is, the number of species that can coexist in equilibrium cannot be greater than the number of limiting resources (Roy and Chattopadhyay, 2007).

ond class of spatially implicit models is commonly used to represent social networks, namely graph networks (Figure 1.2B). Think, for instance of your own social network. Many contacts will live in your own city/country but some live elsewhere. Thus, the information an individual spreads, the culture and norms will to some extent correlate with its spatial location (Helbing, 1995; Nakamaru and Levin, 2004). Note that for applications in ecology or transmission of infections in epidemiology, graph networks can be spatially explicit. However, information transfer in social networks via telephone or internet make a model more detached from the underlying spatial structure.

Mathematical models that include space implicitly have a great value in their respective field but lack a suitable interface to be coupled with other models. Lattice models in contrast, implemented as e.g. cellular automata or coupled map lattices (Figure 1.2C), are convenient for interdisciplinary approaches and are therefore used throughout this thesis (e.g. Clarke et al., 1994; Durrett and Levin, 1994; Nakanishi, 1990; Schweitzer, 2003, for applications in different disciplines). Lattice models with a discrete spatial structure nicely capture human-dominated, terrestrial landscapes with rather homogeneous conditions within a patch and strong heterogeneity between the patches (Deutschman et al., 1993). Patches may vary in geometry, content, heterogeneity and boundary characteristics (García-Moliner et al., 1993), which is why spatially realistic models (geo-referenced, Figure 1.2D) are suitable for case studies. Simplified lattice models deliver more general insight into the relevant fundamental processes, though (Caswell and Etter, 1993; Hanski and Simberloff, 1997). For the sake of completeness, continuous-space modelling techniques should be mentioned as well (Figure 1.2E). Partial differential equations (PDEs) have a long history in physics why the theoretical basis of such models is immense and of great use also in other fields (Alhaji and Rokne, 2014; Caswell and Etter, 1993; Helbing, 1995; Turchin, 1998).

1.4.3 *Temporal dimension*

Let me finally mention some differences between continuous and discrete time models. One may ask why to measure time in discrete units at all, since time is running continuously. And indeed, the amount of population models based on ordinary differential equations (ODEs) exceeds the discrete-time counterpart by far.

Concerning modelling population dynamics, continuous time models are more appropriate if birth and death can be assumed to happen continuously. However, difference equation models are more appropriate for annual species with non-overlapping generations and seasonal breeding (Turchin, 1998; Yodzis, 1989). Examples can be found in both flora and fauna: monocarpic⁹ plants such as bamboo or desert agave and all annual plants have non-overlapping generations. The animal analogue are semelparous insect and fish species, such as mayflies or diadramous¹⁰ fish species, respectively. Seasonal breeders such as shorebirds and waterfowl with synchronized reproduction events, e.g. due to climatic conditions are modelled best in discrete time as well (Kot, 2001). The order of events in such models is important and may produce delayed density dependence, leading to oscillations, or masked effects (Åström et al., 1996; Hilker and Liz,

⁹ Plants that flower once and then die

¹⁰ Migration between freshwater and marine habitats

2013).

In economic models, measuring time in discrete units can be useful to describe agricultural periods, annual sales of firms but also the GDP (Goodwin, 1990; Puu, 2013). A nice feature of coupling different systems is the possibility of a mixture of discrete - and continuous time submodels, often called semi-discrete or hybrid models. However, whenever models are formulated in discrete time, the interpretation of the results needs to be treated with caution. Discrete time systems generally produce a higher complexity such as chaos in only one dimension (Turchin, 1998). This issue will be discussed in **Chapter 3** which provides a comprehensive analysis of a system with coexisting (chaotic) attractors.

1.5 OUTLINE

After the contextual background about conservation and some methodological information about spatio-temporal models used in this dissertation, the chapters are now briefly outlined. The dissertation can be divided into two parts. The first part, consisting of **Chapters 2** and **3**, deals with more theoretical models and ecological concepts relevant to the conservation of spatially structured populations. The generic model formulations make the models applicable to different contexts, though. In **Chapter 2**, the effect of habitat connectivity on population abundance is investigated by an ODE model. The system consists of two logistically growing subpopulations in heterogeneous habitats that are connected by symmetric dispersal. To validate model predictions, we conducted laboratory experiments with *Escherichia coli*. The system has a negative r-K relationship, the relationship between intrinsic growth rates and carrying capacities in the respective environments. This concept partly answers the question of whether dispersal between heterogeneous habitats has a positive or negative effects on the total population density. It was not considered in the conservation literature so far. In **Chapter 3**, a system of two coupled maps is analyzed. The local dynamics can exhibit overcompensation due to a Ricker function and bistability due to an Allee effect. An increased extinction risk due to the Allee effect in combination with the effect of habitat connectivity (symmetric dispersal) is explored. Numerical simulations reveal multiple coexisting attractors and long transients for selected parameter combinations. A new kind of rescue effect, called DIPEE (dispersal induced prevention of essential extinction), is of particular interest for conservation. This mechanism prevents not only extinction of small populations but also large populations that are prone to extinction due to chaotic dynamics.

The second part of the dissertation deals with coupled models concerning land-use decisions in agricultural landscapes in the face of AES. The coupled models account for nonlinearities in the socio-economic as well as in the ecological subsystem and hence promote a better understanding of complex dynamics in coupled human-environment relationships. In **Chapter 4**, a socio-economic model is presented to account for the effect of social norms on the land-use decision-making of farmers. The failure of current AES to promote biodiversity motivates the assumption that habitat quality is not sufficiently increased by current AES. Results-based schemes have a measurable impact on biodiversity whereas the impact of action-oriented schemes is doubtful. Model predic-

tions reflect patterns found in several AES participation data sets: AES participation is more hesitant than suggested by classical economic models but can be effectively promoted by informational campaigns. The question of how to include qualitative information in a quantitative model in general is addressed.

The economic-ecological model presented in **Chapter 5** investigates effects of habitat quality (increased by AES) and habitat composition on the persistence of a population that exhibits an Allee effect. The model accounts for non-linearities in the socio-economic and ecological subsystem and explores different threats for population persistence that act simultaneously. Numerical simulations alter predictions for the cost-effectiveness of AES if the population of concern exhibits an Allee effect. Early conservation measures can protect the population more effectively and spatial agglomeration of habitat can support rescue effects, suggesting land-sparing solutions in the presence of Allee effects. The dissertation ends with a short summary and discussion of the implications and limitations of the results. It gives an outlook on possible future studies related to the research presented in this dissertation and recommendations for management that can be put into practise with available knowledge.

Part I

SPATIAL POPULATION MODELS

HABITAT CONNECTIVITY CAN REDUCE THE TOTAL POPULATION SIZE

I. Vorkamp, C. Kost, M. Hermann, F.M. Hilker

ABSTRACT

Fragmentation of habitats is often considered as a part of habitat degradation and therefore assumed to harm the environment. However, a recent scientific debate about the consequences of habitat fragmentation on biodiversity shows that the single aspects of fragmentation (habitat loss, edge effects and isolation) are not entirely understood. Mathematical theory has shown that dispersal of a population among heterogeneous habitats can increase or reduce the total population density at steady state, depending on the habitat conditions (positive or negative *r-K relationship*, respectively). Positive *r-K* relationships were demonstrated experimentally in the literature but evidence for negative *r-K* relationships is lacking. In this paper, we present experiments with *Escherichia coli* that demonstrate a positive effect of fragmentation, or of isolation in particular, on population size. The experimental data are consistent with the predictions from a mathematical model validated in dispersal experiments. They are the first empirical demonstration of a negative *r-K* relationship. The generic approach we used allows conclusions for a variety of ecological systems and is of particular interest for biological conservation: conservation measures that promote movement between fragmented habitat patches, such as dispersal corridors or stepping stones, which do not counteract habitat loss or edge effects are potentially not (cost-)effective.

2.1 INTRODUCTION

Fragmentation is the breaking up of habitat into smaller, disconnected patches and has increased due to human activities (Turner et al., 2001). It is often considered as a part of habitat degradation and thus to have negative consequences for biodiversity and the environment (Andren, 1994; Debinski and Holt, 2000; Haila, 2002; Margules and Pressey, 2000). However, a review by Fahrig (2017) found more positive than negative biodiversity responses to habitat fragmentation per se (independent of the effects of habitat amount). Positive fragmentation effects on the landscape scale can result from reduced interspecific competition, predator escape or increased habitat diversity (Fahrig et al., 2019; Fischer and Lindenmayer, 2007). This surprising finding has sparked a debate about whether fragmentation has rather negative or positive implications for biodiversity (Fahrig et al., 2019; Fletcher et al., 2018; Miller-Rushing et al., 2019). The contrasting position states that metapopulation theory has clearly shown the increased extinction probability due to fragmentation (Fletcher et al., 2018). Thus, there is no

clear answer to the question of whether habitat fragmentation is beneficial or detrimental for biodiversity (Didham et al., 2012; Fahrig et al., 2019; Miller-Rushing et al., 2019). Part of the problem is that the term fragmentation is used for a range of phenomena and effects are investigated on different spatial scales (Fischer and Lindenmayer, 2007; Hanski, 2015; Lindenmayer and Fischer, 2007).

Typically, fragmentation increases the length of habitat edge and isolation and decreases habitat amount simultaneously (see Figure 3 in Haddad et al., 2015), which poses a challenge for empirical studies to investigate these effects separately (Bunnell, 1999; Fletcher et al., 2018; Hanski, 2015; McGarigal and Cushman, 2002). While there is agreement about negative effects of habitat loss (species-area relationships) and a great number of studies on positive and negative edge effects (e.g. the SLOSS debate during the 1970s), a comprehensive (mechanistic) understanding of connectivity versus isolation effects is lacking (Fischer and Lindenmayer, 2007; Haddad et al., 2015; Hanski, 2015; Tjørve, 2010; Traveset and Riera, 2005; Weddell, 2002). To test for the effect of reduced movement of a population on its abundance without changing habitat amount or habitat edge, mathematical models can give insight. A large body of theoretical studies exists that examine the effect of dispersal among heterogeneous habitats on the total density of a given population. Two main outcomes have been observed: the total population density in connected habitats can be larger or smaller than the total population density of isolated patches (sum of carrying capacities), depending on the strength of intraspecific competition in the respective habitats (Arditi et al., 2015; Franco and Ruiz-Herrera, 2015; Freedman and Waltman, 1977; Holt, 1985; Wu et al., 2020). Intraspecific competition for logistically growing populations is measured by the relationship between the intrinsic growth rates (r) and carrying capacities (K) (Hendriks et al., 2005; Holt, 1985). If intraspecific competition in a highly productive patch (high K) is stronger than in a less productive patch, emigration from the former to the latter can be compensated by rapid growth (high r) in the highly productive patch (Zhang et al., 2017). Hence, the total population density with dispersal is generally larger than in isolated patches, called a *positive r - K relationship* (Figure 2.1a). If intraspecific competition is stronger in the patch with lower carrying capacity, highly productive patches fail to compensate losses due to dispersal. This situation is called a *negative r - K relationship* (Zhang et al., 2017). Two subcases need to be distinguished in this case: dispersal can generally lead to a smaller total population density than in isolated patches (Figure 2.1b) or it can have a non-monotonous effect (Figure 2.1c). Then, weak dispersal leads to larger, whereas strong dispersal leads to smaller total population densities compared to the sum of carrying capacities. A more formal description of the concept will be given in Section 2.2.2.

It is not clear whether or how the parameters r and K are correlated¹. Positive correlation between r and K seems plausible in habitats with fast resource renewal (DeAngelis et al., 2020; Underwood, 2007). However, in habitats where higher temperatures increase growth rates, higher energy needs could lead to lower carrying capacities (Underwood, 2007). When local carrying capacities are limited by available nesting sites or refuges rather than an exploitable resource, per capita growth rates and carrying capacities could also be uncorrelated (DeAngelis et al., 2020).

¹ not to be confused with r - and K -selection

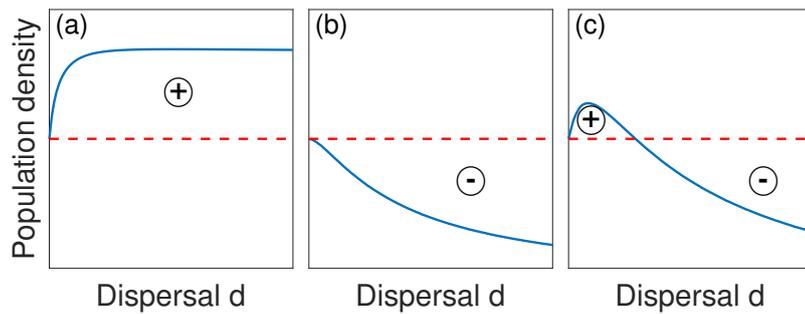


Figure 2.1: Effect of dispersal on the total population density of a logistically growing population after Arditi et al. (2015). Positive or negative r-K relationships lead to positive (a), negative (b) or changing (c) effects of dispersal on the total population density (blue solid) compared to the sum of carrying capacities (red dashed line). Sign of effect is indicated by circled plus and minus symbols.

Since it is not clear whether highly productive habitats automatically promote rapid growth, empirical evidence for positive and negative r-K relationships is even more scarce (Ives et al., 2004; Mallet, 2012; Zhang et al., 2017). We combine a numerical analysis of a generic mathematical model with laboratory-based experiments of the organism *Escherichia coli* to give the first empirical evidence for a negative r-K relationship. Our results corroborate that movement between habitats can be detrimental if the r-K relationship of the two habitats is negative. This result is supported by both model simulations and experimental data and extends the list of possible positive consequences of fragmentation.

2.2 MATERIAL AND METHODS

The effect of dispersal on the long-term population density of a single species in spatially heterogeneous habitats is investigated. The situation is reduced to two habitats that differ with regards to the habitat quality which determines the growth conditions (see Figure 2.2 for a schematic illustration). A proportion of individuals is assumed to move between the habitat patches. The effect of habitat connectivity is investigated by a systematical test of different dispersal regimes (proportions).

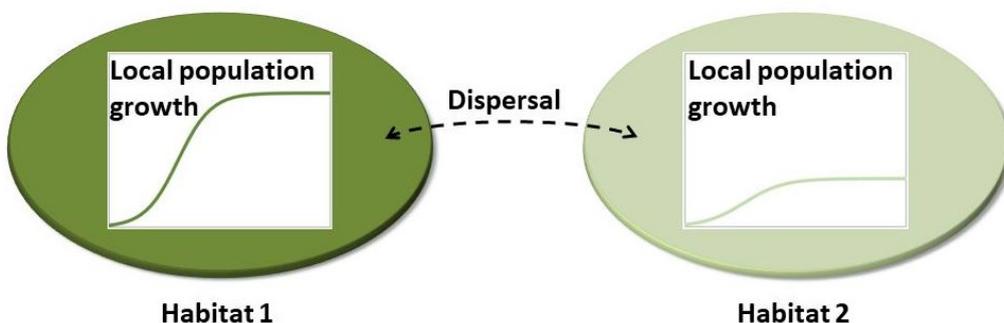


Figure 2.2: Schematic illustration of this study. Different colors represent heterogeneous habitat conditions.

2.2.1 The model

The growth process in the mathematical model is realized by the Baranyi model (Baranyi and Roberts, 1994), a well-known model for bacterial growth. This model can capture both the initial lag phase² and the following logistic growth. Logistic growth models are typically used for bacterial growth (Gibson et al., 1987; Zwietering et al., 1990) but are more generally widely used model to describe density dependent growth processes of populations. A dispersal term in the model accounts for an exchange of a proportion of the population between the two habitat patches:

$$\begin{aligned}\frac{dN_1}{dt} &= \frac{Q_1}{1+Q_1} r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - d(N_1 - N_2), \\ \frac{dN_2}{dt} &= \frac{Q_2}{1+Q_2} r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - d(N_2 - N_1).\end{aligned}\tag{2.1}$$

The population density in patch i is described by N_i with initial conditions $N_i(0) = N_{i,0}$. In the following, patch N_1 denotes the highly productive habitat and N_2 the less productive habitat. Parameters r_i and K_i denote the intrinsic growth rate and the carrying capacity in the respective patch, and d is the (symmetric) dispersal rate between patches. State variable Q_i with initial conditions $Q_i(0) = Q_{i,0}$ accounts for the physiological state of the population, and the term $\frac{Q}{1+Q} \in [0, 1]$ describes how long it takes the population to adapt to the new habitat. Thus, the term has a large impact on the transient dynamical behaviour but no effect in the long term. The duration of the lag phase is assumed to be inversely proportional to r_i and grows exponentially:

$$\frac{dQ_i}{dt} = r_i Q_i.\tag{2.2}$$

Note the simplifying assumption that Q_i only depends on the nutrient supply in patch i and is not affected by dispersal. It is known that the lag phase depends on many factors such as the current environment, the inoculation environment, the stage of the cells and other factors (Swinnen et al., 2004). Following the principle of parsimony, these effects are neglected.

In a preliminary experiment, growth kinetics were fitted to obtain parameters r_i and K_i for the two growth environments. To do so, the analytical solution Baranyi and Roberts (1994) of Equations (2.1)-(2.2) without dispersal (i.e. $d = 0$) was used:

$$N_i(t) = \frac{K_i}{1 + \left(\frac{K_i}{N_{i,0}} - 1\right) \exp(-r_i A_i(t))},\tag{2.3}$$

with

$$A_i(t) = t + \frac{1}{r_i} \ln \left(\frac{\exp(-r_i t) + Q_{i,0}}{1 + Q_{i,0}} \right).$$

² If bacterial colonies are put into fresh medium and then incubated, their growth is initiated by a lag phase in which the bacteria grow less due to adjustment to the new conditions, e.g. temperature or amount of resources (Madigan et al., 2020).

Note that, in a strict sense, a continuous-time model with simultaneous occurrence of growth and dispersal, does not perfectly coincide with the experimental design, in which the dispersal steps occur at discrete time steps for handling reasons. This discrepancy can lead to slightly different dynamics. However, according to Zhang et al. (2017), qualitative errors should remain small. The aim of fitting the mathematical model to the growth kinetics experiment is to determine the nature (positive or negative) of the r-K relationships.

2.2.2 The r-K relationship

The logistic growth model makes several assumptions for population growth. Firstly, the per capita growth rate, which is given by

$$\frac{1}{N} \frac{dN}{dt} = r \left(1 - \frac{N}{K} \right) =: F(N),$$

has its maximum for very low population densities at the intrinsic growth rate r . Secondly, there exists an upper limit K of population density due to a limited amount of resources or energy which is approached in the long term. Thirdly, intraspecific competition between individuals leads to negative density dependence. Following Holt (1985), it can be quantified by

$$\frac{dF}{dN} = -\frac{r}{K}.$$

Thus, the larger r/K , the stronger is the intraspecific competition in a habitat (Hendriks et al., 2005). By comparing the r-K relationships of a population in two habitats, one gets information about whether dispersal increases or decreases the overall population density at steady state (Arditi et al., 2015; Freedman and Waltman, 1977; Holt, 1985). A positive r-K relationship (in the following rK_+) generally leads to a larger total population density with dispersal than the sum of carrying capacities (Figure 2.1a, Table 2.1 for parameter combinations). A negative r-K relationship can reduce the total population density (in the following rK_-) compared to the sum of carrying capacities (Figure 2.1b, Table 2.1 for parameter combinations) or it can have a non-monotonous effect (in the following rK_{\pm}). In the latter case, weak dispersal ($0 < d < d_{\text{crit}}$) leads to larger, whereas strong dispersal ($d > d_{\text{crit}}$) leads to smaller total population densities compared to the sum of carrying capacities (Figure 2.1c, Table 2.1 for parameter combinations). The critical value d_{crit} according to Arditi et al. (2015) is $d_{\text{crit}} = (r_i - r_j) / [(K_i/r_i - K_j/r_j) \cdot (r_i/K_i + r_j/K_j)]$.

The r-K relationship makes qualitative predictions about the effect of dispersal on the overall population density. Hence, it can help to answer the question of whether fragmentation is harmful or beneficial to populations. However, no general conclusions can be drawn for how pronounced the effects are in real biological systems. To this end, we make a contribution by our experimental approach. Note that, strictly speaking, we are not considering logistic growth in this paper since the Baranyi model includes a lag phase which is typical for bacterial growth but not part of the logistic growth model. However, since the lag phase is only relevant in the transient growth phase and does not

affect equilibrium population densities, the proofs in Arditi et al. (2015) also hold for the Baranyi model.

Table 2.1: Conditions for a positive or a negative r-K relationship between two habitat patches ($i \neq j$) after Arditi et al. (2015).

Positive r-K relationship (rK_+)	$K_i > K_j$	$r_i/K_i \geq r_j/K_j$	$r_i > r_j$
Negative r-K relationship (rK_-)	$K_i > K_j$	$r_i/K_i < r_j/K_j$	$r_i \leq r_j$
Negative r-K relationship (rK_{\pm})	$K_i > K_j$	$r_i/K_i < r_j/K_j$	$r_i > r_j$

2.2.3 Bacterial strains and cultivation conditions

For all experiments, populations of the bacterium *Escherichia coli* BW25113 (Baba et al., 2006) were used. Cells were grown in nutrient-rich (i.e. full lysogeny broth (LB) growth medium (LB Lennox, Carl Roth GmbH)) or a nutrient-poor medium (i.e. LB Lennox diluted in ratio 1:100 with NaCl (5 gL⁻¹) for osmotic pressure). Bacterial populations were cultivated at 30 °C and liquid cultures shaken at 200 rpm.

To initiate experiments, bacterial strains were streaked on fresh LB-agar plates and incubated for 18 h or until single colonies showed sufficient size for inoculation of liquid cultures. Individual colonies were used as biological replicates to inoculate 10 mL precultures of the two growth environments in test tubes. To minimize bacterial growth during the plating process, cultures were diluted using saline solution (5 gL⁻¹ NaCl).

2.2.3.1 Growth kinetics

After 3 h of inoculation, precultures were adjusted to an optical density (OD) of 0.001 at 600 nm as determined via spectrophotometry in a plate reader (Spectramax M5, Applied Biosystems) and diluted 1,000-fold. 14 precultures of 8 replicates each in 1.5 mL of nutrient-rich and nutrient-poor medium were used to start the experiment. All cultures were incubated in 96 deep-well plates (maximal volume: 2 ml, Thermo Scientific Nunc). The number of colony-forming units (CFUs) per mL culture volume was evaluated at one hour intervals (13 hours total) by drop plating the serially-diluted culture on LB agar plates.

2.2.3.2 Dispersal experiment

After 3 h of inoculation, precultures were adjusted to an OD of 0.002 at 600 nm as determined via spectrophotometry in a plate reader after 3 h (Spectramax M5, Applied Biosystems). Note that the initial OD is chosen close to the carrying capacity for handling reasons. Precultures were divided in four experimental groups, each consisting of one culture in 1.5 mL nutrient-rich and one culture in 1.5 mL nutrient-poor medium. Groups differed in the amount of cells that were transferred between environments: (d_1) no transfer between environments, (d_2) transfer of 1/5 of the culture to the other environment, (d_3) transfer of 2/3 of the culture to the other environment and (d_4) transfer of the whole culture to the other environment under the assumption of complete mixing.

Four replicates of each group were used to start the experiment. Besides differences in the dispersal regime, all groups were treated in an identical way during the experiment. Cultures were incubated in microtubes (max. volume: 2 mL, eppendorf) and transferred every 1.5 h for a total of six transfers. To realize transfer of cells without mixing the media, cultures were split according to the dispersal regime (e.g. for d_2 : split 1.5 mL into 1.2 mL and 0.3 mL), centrifuged twice (each 2 min, 4,000 rpm), resuspended in the same volume of the corresponding medium and reassembled. At the end of each cycle, the number of CFUs per mL culture volume was determined by drop plating the serially-diluted culture on LB agar plates.

2.2.4 Parameter estimation and statistical analysis

Parameter estimation was performed using the MATLAB R2020a Curve Fitting Toolbox and lsqnonlin of the MATLAB R2020a Optimization Toolbox.

Bacterial counts are presented on a logarithmic scale. Thus, parameters r_i and K_i are obtained by fitting Equation (2.A.1) in Appendix 2.A to log-transformed data generated from growth kinetics in isolated media (nutrient-rich and nutrient-poor). $Q_{i,0}$ was obtained by fitting numerical solutions of System (2.1) to data generated in the dispersal experiments (d_1 - d_4).

The statistical analysis was performed using the MATLAB R2020a Statistics Toolbox. Normal distribution of data was analyzed using the Lilliefors test. Homogeneity of variances was determined by applying the Brown-Forsythe test and variances were considered to be homogeneous when $p > 0.05$. Independent sample t-tests were performed against the null hypothesis that the total population density monotonically decreases with decreasing dispersal proportions. For the growth kinetics, the sample size $n = 8$ refers to the number of independent bacterial populations analysed. In the dispersal experiment, the sample size $n = 8$ results from four independent bacterial populations, two replicates each. Asterisks indicate significant differences in pairwise comparisons (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

2.3 RESULTS

In a preliminary experiment, growth kinetics of *E.coli* for the two environments were conducted to find growth parameters for the model (see Figure 2.B.1 in Appendix 2.B). The dispersal experiment was performed to generate temporal dynamics for population growth under four dispersal regimes (d_1 - d_4). Final bacterial concentrations were then used to test for the effect of dispersal on the long-term total population density ($N_{1,t_{\text{end}}} + N_{2,t_{\text{end}}}$). Numerical simulations of the model were compared with experimental outcomes.

2.3.1 Model calibration reveals negative r-K relationship

To analyze the experimental data with respect to the r-K relationships, parameter values for the model were fitted to the data (Table 2.2). Patch N_1 provides better (larger r and K) growth conditions for the bacteria than patch N_2 . However, intraspecific competi-

tion (measured by r/K) appears to be stronger in patch N_2 than in N_1 . This parameter combination constitutes a negative r-K relationship with non-monotonous effect (rK_{\pm}). Thus, a larger total population density than the sum of carrying capacities for dispersal rates smaller than some critical value d_{crit} should be observed. For dispersal rates $d > d_{\text{crit}}$, the r-K relationship predicts a total population density smaller than the sum of carrying capacities.

Table 2.2: Fitted parameter values for Model (2.1) have a negative r-K relationship (rK_{\pm}).

Patch	Q_0	r	K	r/K
N_1	$10^{4.8425}$	1.376	10^{10}	1.376×10^{-10}
N_2	$10^{-2.69}$	1.201	$10^{7.7}$	2.396×10^{-8}

2.3.2 Two become one

A time series of population growth of *E.coli* under different dispersal regimes was generated to investigate how the amount of dispersal changes the dynamical behaviour of the system. The experimental data for dispersal regime (d_1) without transfer of cells shows a saturation course over time to the carrying capacity in the respective environment (Figure 2.3a). The final CFU in patch N_1 is more than two orders of magnitude larger (logarithmic scale) than in patch N_2 . With transfer between the patches (d_2 - d_3), cell densities in the two patches differ less than in the case without transfer (Figure 2.3b-c). The final CFU in N_1 is about one (Figure 2.3b) and less than one (Figure 2.3c) order of magnitude larger than in N_2 . If all cells are transferred (d_4), the final CFU is approached in a fluctuating manner (Figure 2.3d). However, the amplitude of fluctuations becomes smaller. See, for instance, the CFU in N_2 decreases after 1.5 h from around 7.5 to 6.5. In contrast, the decrease after 7.5 h is almost negligible, indicating that the system likely attains a stable equilibrium in the long-term.

Strikingly, model solutions strongly matched with experimental data. The long lag phase in patch N_2 produced an s-shaped curve in the simulations (Figure 2.3, orange dashed line). Due to the good growth conditions in N_1 and the fact that bacteria were in their exponential growth phase, the initial lag phase was not visible in the simulations (Figure 2.3, blue solid line). The qualitative behaviour of the model solution for dispersal regime (d_4) slightly differs from the dynamics shown in the data in terms of showing no fluctuations (Figure 2.3d). However, the final densities reached by populations of all dispersal regimes were captured well. Overall, both model simulations and empirical data show that population dynamics in isolated patches were rather independent from each other, yet the two patches started to behave more like one as the rate of dispersal between them increased.

2.3.3 Dispersal reduces population density in the long-term

Given that populations approached equilibrium towards the end of the experiment, the final density reached provides information on how the different dispersal regimes will

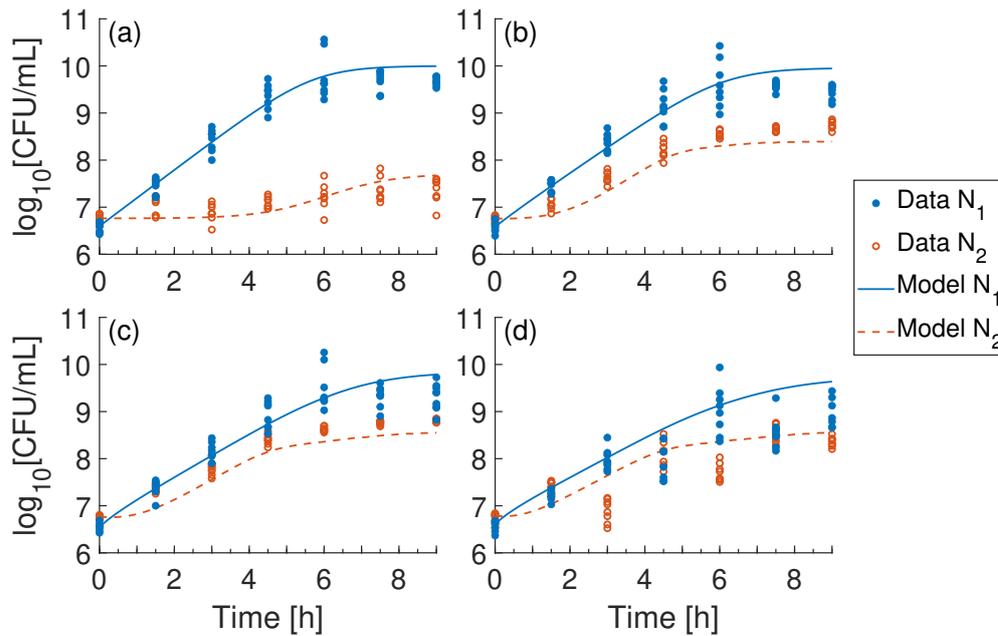


Figure 2.3: Two isolated patches show distinct temporal growth dynamics (a). Due to dispersal, the growth curves approach each other (b-d). Experimental data for temporal dynamics of *E. coli* in nutrient-rich environment (blue, filled) and nutrient-poor environment (red, empty) under the dispersal regimes d_1 - d_4 (a-d respectively). Solid and dashed lines represent model predictions with parameter values shown in Table 2.2.

affect total population density in the long-run (Figure 2.4, boxplot). The total cell density was largest in two isolated patches and monotonically decreasing with increasing dispersal. The model confirms the decreasing trend of the total population density after 9 hours for increasing dispersal rates d . Since equilibrium is not yet fully achieved at the end of the experiments, model simulations were additionally performed until the system can be assumed to be at steady state (Figure 2.4, red dashed line). The qualitative results of this analysis remain the same.

At first glance, the monotonically decreasing trend of the total population size, which was observed in both simulated and experimental results, does not fit the theory of the r-K relationship. The fitted growth parameters in the model suggest a negative r-K relationship with non-monotonous effect (rK_{\pm}). Thus, a larger total population density than the sum of carrying capacities for dispersal rates smaller than some critical value d_{crit} should be observed. Indeed, the model solution reveals a slightly larger total population density for very small dispersal rates ($0 < d < d_{\text{crit}} \approx 0.00102$) than in isolated patches (Figure 2.4, inset). This result shows that even if rK_{\pm} predicts larger total population densities than the sum of carrying capacities for small dispersal rates, the concept does neither make any general statement about the magnitude of the critical dispersal rate d_{crit} nor about the magnitude of population increase. Overall, our model system is an example in which dispersal reduces the total population density in almost all cases.

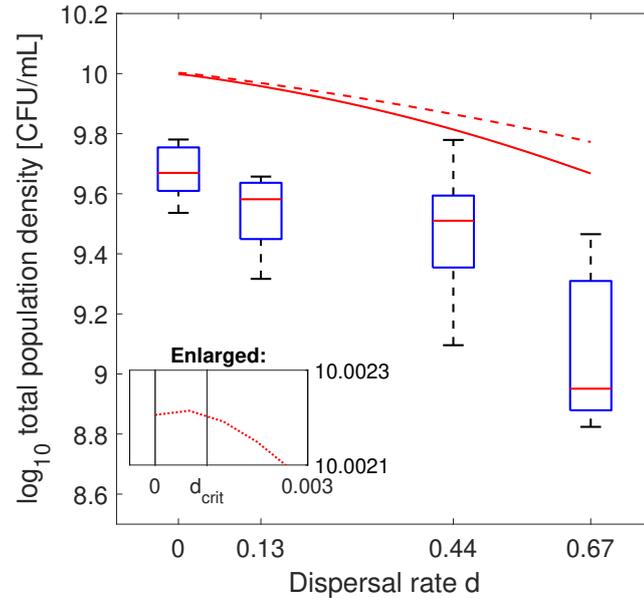


Figure 2.4: Total population density was largest in two isolated patches (significant in comparison of (d_1) with all other regimes; (d_2) : $*p = 0.0182$, (d_3) : $*p = 0.0234$ and (d_4) : $**p = 0.0021$) and monotonically decreasing with increasing dispersal (not significant for (d_2) and (d_3) : $p = 0.1859$, significant for (d_3) and (d_4) : $*p = 0.0163$). The figure shows the CFU after 9 h (boxplots) for dispersal regimes (d_1-d_4) and simulated total population density at $t_{\text{end}} = 9$ (solid red line) and $t_{\infty} = 100$ (dashed red line) with Model (2.1) with parameter values shown in Table 2.2. Note that experimental dispersal regimes were transformed to dispersal rates [h^{-1}].

2.4 DISCUSSION

This study investigated the effect of dispersal among two habitats with heterogeneous resource availability on the total population density of a single species. We combined a mathematical model with laboratory experiments and showed that dispersal reduced the overall population density compared to two isolated patches. A mechanistic explanation for this result was found to be a negative r-K relationship (rK_{\pm}) for the population in the two habitat patches (Arditi et al., 2015). To our knowledge, this is the first experimental demonstration of a negative r-K relationship. In combination with previous empirical studies that reported positive effects of dispersal on the total population size (Ives et al., 2004; Zhang et al., 2017, 2015), we corroborate existing theory of r-K relationships by giving an empirical example.

If reduced dispersal between habitats is assumed to be caused by reduced habitat connectivity, our result can be interpreted as a mechanism for positive effects of fragmentation. The scope of this paper is not to argue for positive or negative effects of fragmentation in general or to question effects of fragmentation caused by other factors (Hanski, 2015). It is well-known that the consequences of fragmentation are determined by many other factors as well, e.g. negative/positive edge effects, functional connectivity and landscape complementation (e.g. Didham et al., 1996; Fahrig, 2017; Fischer and Lindenmayer, 2007; Haddad et al., 2015; Villard and Metzger, 2014). However, even though positive and negative effects of habitat isolation are known, ranging from in-

breeding depression (genetic variability) and relaxation over range shifts in response to climate change to a spread of the extinction risk (Driscoll et al., 2013; Fischer and Lindenmayer, 2007; Soulé et al., 2004; Weddell, 2002), the relative growth conditions in heterogeneous habitats (r-K relationship) were not identified to have an impact on fragmentation effects so far. On that basis, our results challenge the paradigm that fragmentation is always detrimental to biodiversity (Fischer and Lindenmayer, 2007; Foley et al., 2005; Haila, 2002; Hanski, 2015). We suggest a separate investigation of isolation, habitat edge and habitat amount instead (Andren, 1994; Didham et al., 1996; Hobbs and Yates, 2003). In practice, it may be useful to avoid fragmentation because fragmentation is almost always accompanied by habitat loss (Fletcher et al., 2018), which indeed was often found to cause a reduction of biodiversity and population abundances (Andren, 1994; Debinski and Holt, 2000; Fahrig, 2003; Gibbons et al., 2000; Kerr and Deguise, 2004; McGarigal and Cushman, 2002; Sala et al., 2000; Stuart et al., 2004). However, this connection is not necessarily given if fragmentation is to be reversed.

Much effort in biological conservation is put into measures that reduce fragmentation by bridging the gaps between habitats, e.g. by dispersal corridors or stepping stones (Fischer and Lindenmayer, 2007; Weddell, 2002). Dispersal corridors allow movement between habitat fragments to increase overall habitat connectivity and were found to increase both the species richness and population densities in some cases (Debinski and Holt, 2000; Haddad and Baum, 1999; Phillips et al., 2008). However, given that corridors can also be disadvantageous, in terms of promoting disease spread or increase predation pressure, there are good reasons to doubt the wisdom of corridors, at least as a ubiquitous solution (Åström and Pärt, 2013; Barrett et al., 1995; Debinski and Holt, 2000; Fahrig, 2003, 2017; Fischer and Lindenmayer, 2007; Hobbs and Yates, 2003; Simberloff et al., 1992; Turchin, 1998). Moreover, corridors as a measure that do not counteract the more pronounced problem of habitat loss may not be (cost-)effective (Fischer and Lindenmayer, 2007; Miller-Rushing et al., 2019). In contrast, measures focusing on the restoration of destroyed habitat may not increase connectivity but can still be valuable (Villard and Metzger, 2014).

Some implicit assumptions were made in our study and will be discussed in the following. The two habitats were chosen such that the population can persist in each patch. However, some species have specific requirements regarding habitat size (e.g. home ranges), which could be undermined by fragmentation (Andren, 1994; Hanski, 2015; Margules and Pressey, 2000). Thus, predicting the effect of fragmentation requires detailed knowledge on the spatial scale. Our results hold on the population scale where fragmentation occurs within populations connected by animal movement but probably not when fragmentation occurs within individuals' home-ranges (Franklin et al., 2002; Hanski, 2015). Another assumption in our model that may need to be adapted for certain species is that of symmetric passive dispersal to model population movement which will unlikely hold for animal populations. Nevertheless, dispersal of populations of both plants and animals over long time scales can often be represented as diffusive (DeAngelis et al., 2016a).

Despite these limitations, our combined approach of a mathematical model with laboratory experiments made a step towards a more mechanistic understanding of fragmen-

tation effects. The simple model formulation allows rigorous mathematical proof for the implications of positive and negative r-K relationships in the sense of Arditi et al. (2015). The experimental model validation gives first empirical demonstration of a negative r-K relationship.

To investigate how pronounced negative r-K relationships are in other systems, we reviewed empirical studies that report laboratory data of logistically growing populations under several types of heterogeneous environmental conditions. Most of the studies tested for the effect of toxins in the environment or bacterial food contamination under different temperatures. Hence, in most of the studies the aim was not to investigate the effect of dispersal on the total population density. We analyzed the data in order to examine whether r-K relationships were positive or negative and found broad evidence for all cases (Table 2.3, see Appendix 2.C for further information). Apparently, there is no general pattern for r-K relationships that holds for all species (DeAngelis et al., 2016b) which indicates that the negative r-K relationship found in this study is not an exception but occurs in many biological systems. Hence, beneficial effects of fragmentation may be expected more widely beyond the system considered here.

Table 2.3: Evidence for positive r-K relationships (rK_+) and/or negative r-K relationships (rK_- , rK_{\pm}) in empirical studies. x: evidence, **X**: most evidence (more than three times the number of examples or over thirty more examples), otherwise no evidence. Note that studies differ with respect to the number of tested r-K relationships.

Reference	Modeled species	rK_+	rK_-	rK_{\pm}	Heterogeneity condition
Valle et al. (1989)	<i>Nephotettix</i> spp	X	x	x	Temperature
Bell (1990)	<i>Chlamydomonas</i>	x	X	x	Mineral nutrients
Dumont et al. (1995)	<i>Anuraeopsis fissa</i>			x	Food density
Hendriks et al. (2005)	Several	x	x	X	Toxin concentration
Underwood (2007)	<i>Chaetosiphon fragaefolii</i>	x	X	X	Host plant
Salari and Salari (2017)	<i>Saccharomyces cerevisiae</i>	x	X	X	pH and dissolving oxygen
Zhang et al. (2017)	<i>Saccharomyces cerevisiae</i>	x			Culture medium
Bernhardt et al. (2018)	<i>Tetraselmis tetrahele</i>	X	X	x	Temperature
This study	<i>Escherichia coli</i>			x	Culture medium

ACKNOWLEDGEMENTS

The authors thank Jan Hendriks for the provision of the raw data to test for r-K relationships. CK was financially supported by the German Research Foundation (DFG, KO 3909/4-1, SFB 944 -TP 19) and the international graduate school EvoCell (funded by the University of Osnabrück).

APPENDIX

2.A BARANYI MODEL: LOG-TRANSFORMATION

To fit Model (2.1) without dispersal ($d = 0$) to the experimental data, it needs to be log-transformed. Let $y_i = \log_{10}(N_i)$. Then

$$\frac{dy_i}{dt} = \frac{d \log_{10}(N_i)}{dt} = \frac{1}{\ln(10)} \frac{1}{N_i} \frac{dN_i}{dt},$$

where \ln is the natural logarithm. Let $q_i = \log_{10}(Q_i)$ and $y_{i,max} = \log_{10}(K_i)$. It follows:

$$\begin{aligned} \frac{dy_i}{dt} &= \frac{r_i}{\ln(10)(1 + 10^{-q_i})} (1 - 10^{y_i - y_{i,max}}), \\ \frac{dq_i}{dt} &= \frac{r_i}{\ln(10)}. \end{aligned}$$

The exact solution on a log-scale is

$$y_i(t) = y_{i,max} - \log_{10} \left(1 + \frac{10^{y_{i,max} - y_{i,0}} - 1}{\exp(r_i a_i(t))} \right) \quad (2.A.1)$$

with

$$a_i(t) = t + \frac{1}{r_i} \ln \left(\frac{\exp(-r_i t) + 10^{q_{i,0}}}{1 + 10^{q_{i,0}}} \right),$$

$y_{i,0} = \log_{10}(N_{i,0})$ and $q_{i,0} = \log_{10}(Q_{i,0})$.

2.B GROWTH KINETICS

The analytical solution of the log-transformed Baranyi model was fitted to the growth kinetics of *E.coli* in two isolated patches to obtain growth parameters for the respective environment (Figure 2.B.1). Both kinetics show the typical sigmoid curve, whereby the plot for the nutrient-rich environment (Figure 2.B.1, blue solid line) has not yet reached the carrying capacity visibly. However, after conducting preliminary experiments (not shown), we conclude that the curve is close to carrying capacity K_1 after 13 hours.

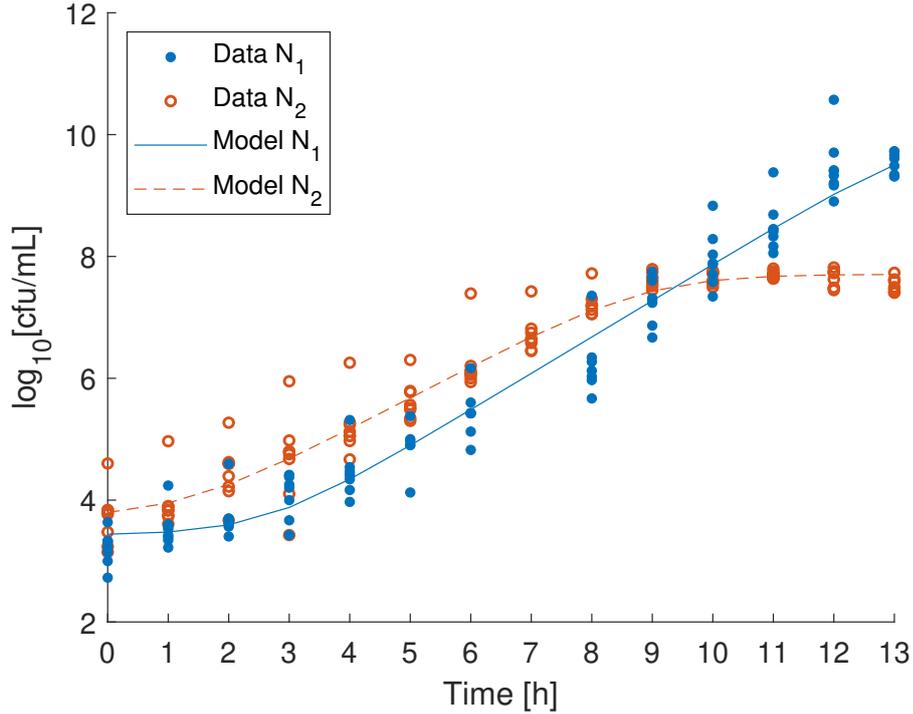


Figure 2.B.1: Growth kinetics of *E. coli* over time (at 30°) in nutrient-rich (blue, filled dots) and nutrient-poor environment (orange, empty dots). Gap in data of N_1 at $t = 7$ h due to failed drop plating. Model fits were performed with the analytical solution of the log-transformed Baranyi model without dispersal (Equation (2.A.1)). Fitted parameters: $r_1 = 1.376$, $K_1 = 10^{10}$, $r_2 = 1.201$, $K_2 = 10^{7.7}$. Fit quality for N_1 ($R^2 = 0.9899$) is slightly lower than for N_2 ($R^2 = 0.9937$). Sample size $n = 8$ was the same for both kinetics.

2.C DATA ANALYSIS FOR R-K RELATIONSHIP

To investigate how pronounced positive and negative r-K relationships are in real biological systems, we analyzed empirical studies that report laboratory data of logistically growing populations under several types of heterogeneous environmental conditions. Where parameters were given in the references, we directly used the parameters for the analysis. Otherwise, we fitted data to the logistic model or the Baranyi model (with lag phase), to obtain parameter values. We analyzed the data by pairwise comparison of the terms for intraspecific competition (r/K). The outcome will be documented in upper triangular matrices in the following manner:

$$\begin{matrix}
 & A & B & C \\
 A & & + & - \\
 B & & & \pm \\
 C & & &
 \end{matrix}$$

In this example there are three habitats. A, B and C denote the consecutive rows in the respective table. Habitats A and B have a positive r-K relationship, B and C have a

negative r-K relationship (rK_{\pm}) and A and C have a negative r-K relationship (rK_{-}).

***Nephotettix spp* (Valle et al., 1989)**

Table 2.C.1 shows mostly positive (rK_{+}) but also negative (rK_{-} and rK_{\pm}) r-K relationships.

Table 2.C.1: r and K values (logistic model) for different temperatures in Valle et al. (1989) to test for r-K relationship.

Species	r	K	r/K	r-K relationships
<i>N. nigropictus</i>	0.1435	1269	0.11308×10^{-3}	$\begin{pmatrix} + & + \\ & \pm \end{pmatrix}$
	0.1733	1315.6	0.13173×10^{-3}	
	0.186	1413.9	0.13155×10^{-3}	
<i>N. virescens</i>	0.1445	1184.8	0.12196×10^{-3}	$\begin{pmatrix} + & + \\ & \pm \end{pmatrix}$
	0.1726	1255.5	0.13748×10^{-3}	
	0.199	1580.1	0.12594×10^{-3}	
<i>N. cincticeps</i>	0.161	1428.5	0.11271×10^{-3}	$\begin{pmatrix} + & - \\ & - \end{pmatrix}$
	0.1809	1506	0.12012×10^{-3}	
	0.1845	1374.4	0.13424×10^{-3}	
<i>N. malayanus</i>	0.1257	543.3	0.23136×10^{-3}	$\begin{pmatrix} + & + \\ & + \end{pmatrix}$
	0.1549	610	0.25393×10^{-3}	
	0.1669	615.4	0.27121×10^{-3}	

***Chlamydomonas* (Bell, 1990)**

Table 2.C.2 shows mostly negative (rK_{-}) r-K relationships, few positive r-K relationships (rK_{+}) and one negative (rK_{\pm}) r-K relationship.

Table 2.C.2: r and K values (logistic model) in environments with different nutrient supply in Bell (1990) to test for r-K relationship.

r	K	r/K	r-K relationships
2.75	4.74	0.5794	$\begin{pmatrix} - & - & - & - & - & + & - \\ & - & - & - & - & - & - \\ & & - & - & - & + & - \\ & & & - & - & - & - \\ & & & & - & + & + \\ & & & & & \pm & - \\ & & & & & & + \\ & & & & & & & + \end{pmatrix}$
2.50	5.19	0.4819	
2.79	4.71	0.5929	
2.17	5.74	0.3784	
4.04	4.22	0.9572	
4.18	4.16	1.0046	
4.89	5.01	0.9750	
4.18	4.36	0.9594	

Anuraeopsis fissa (Dumont et al., 1995)

Table 2.C.3 shows negative (rK_{\pm}) r-K relationships.

Table 2.C.3: r (linear regression for exponential growth phase) and mean K values (measured) in environments with different food supply in Dumont et al. (1995) to test for r-K relationship.

r	K	r/K	r-K relationships
0.454	282	1.6×10^{-3}	$\left(\begin{array}{cccc} \pm & \pm & \pm & \pm \\ & \pm & \pm & \pm \\ & & \pm & \pm \\ & & & \pm \\ & & & \pm \end{array} \right)$
0.4808	408	1.2×10^{-3}	
0.5344	666	0.8×10^{-3}	
0.6416	1270	0.5×10^{-3}	
0.856	1989	0.4×10^{-3}	

Meta-analysis (Hendriks et al., 2005)

Meta-analysis of 95 intrinsic growth rates and carrying capacities of populations affected by toxic and other stressors. Groups of algae, rotifers, annelids, crustaceans, insects, arachnids and others were tested. Ratios of exposed and control growth parameters are compared for all species. Single parameter values are not available. Figure 2.C.1 shows mostly negative (rK_{\pm}) but also positive and negative (rK_{-}) r-K relationships.

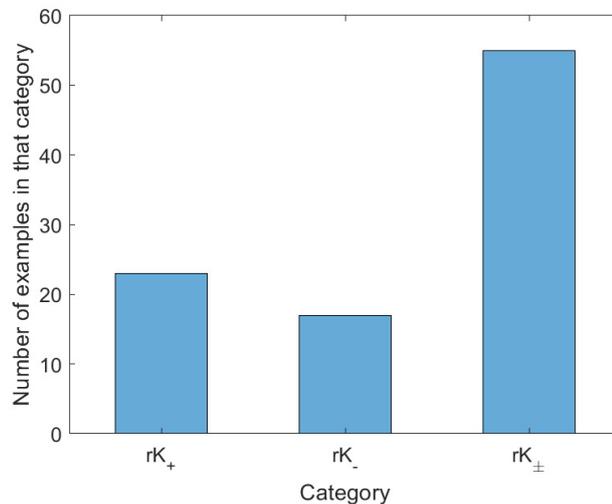


Figure 2.C.1: r - and K -ratios in environments with and without toxin/stressor in Hendriks et al. (2005) determine the r-K relationship. Categories as defined in Section 2.2.2.

Chaetosiphon fragaefolii (Underwood, 2007)

Table 2.C.4 shows mostly negative (rK_{-} and rK_{\pm}) r-K relationships, only few positive r-K relationships (rK_{+}).

Table 2.C.4: Maximum likelihood estimates (logistic model) of r and K values on different host plants in Underwood (2007) to test for r-K relationship. Note that parameters were obtained by using webplot digitizer since no raw data was available.

r	K	r/K	r-K relationship
0.176	8.2	2.146×10^{-2}	$\left(\begin{array}{cccccccccc} - & - & - & - & - & \pm & \pm & - & - & \pm \\ & + & + & \pm \\ & & \pm \\ & & & - & \pm & \pm & \pm & \pm & - & \pm \\ & & & & \pm & \pm & \pm & \pm & - & \pm \\ & & & & & + & \pm & - & - & \pm \\ & & & & & & - & - & - & - \\ & & & & & & & - & - & \pm \\ & & & & & & & & - & + \\ & & & & & & & & & + \\ & & & & & & & & & + \end{array} \right)$
0.068	23.83	2.853×10^{-3}	
0.099	25.45	3.890×10^{-3}	
0.128	32.93	3.887×10^{-3}	
0.126	229.69	5.486×10^{-4}	
0.145	345.79	4.193×10^{-4}	
0.245	554.8	4.416×10^{-4}	
0.198	575.12	3.443×10^{-4}	
0.141	723.16	1.950×10^{-4}	
0.104	884.5	1.176×10^{-4}	
0.213	887.97	2.399×10^{-4}	

***Saccharomyces cerevisiae* (Salari and Salari, 2017)**

Table 2.C.5 shows almost exclusively negative (rK_- and rK_{\pm}) r-K relationships.

Table 2.C.5: Fitted r and K values (Baranyi model) in environments with different pH values and dissolved oxygen in Salari and Salari (2017) to test for r-K relationship. Note that data was analyzed using webplot digitizer since no raw data was available.

r	K	r/K	r-K relationship
0.7259	0.3129×10^{11}	0.2320×10^{-10}	$\left(\begin{array}{cccccccccc} + & + & \pm & \pm & \pm & \pm & - & \pm \\ & - & - & - & - & - & - & - \\ & & - & - & - & - & - & - \\ & & & \pm & \pm & \pm & - & - \\ & & & & \pm & \pm & - & - \\ & & & & & - & - & - \\ & & & & & & - & - \\ & & & & & & & \pm \\ & & & & & & & \pm \end{array} \right)$
1.5448	0.3670×10^{11}	0.4209×10^{-10}	
1.5412	0.3883×10^{11}	0.3969×10^{-10}	
0.7633	0.4286×10^{11}	0.1781×10^{-10}	
0.8098	0.5048×10^{11}	0.1604×10^{-10}	
1.0338	0.7251×10^{11}	0.1426×10^{-10}	
1.0275	0.7560×10^{11}	0.1359×10^{-10}	
0.6545	1.1193×10^{11}	0.0585×10^{-10}	
0.7272	1.3256×10^{11}	0.0549×10^{-10}	

***Tetraselmis tetrahele* (Bernhardt et al., 2018)**

Table 2.C.6 shows mostly positive (rK_+) and negative (rK_-) r-K relationships.

Table 2.C.6: Fitted r and K values (logistic model) in environments with different temperatures in Bernhardt et al. (2018) to test for r-K relationship.

r	K	r/K	r-K relationship
0.4231	0.3711×10^4	0.1140×10^{-3}	$\left(\begin{array}{cccc} - & \pm & - & - \\ & + & + & + \\ & & - & - \\ & & & + \end{array} \right)$
0.1025	1.3157×10^4	0.0078×10^{-3}	
1.4590	1.7470×10^4	0.0835×10^{-3}	
0.1882	1.9992×10^4	0.0094×10^{-3}	
0.2379	2.0073×10^4	0.0119×10^{-3}	

MULTIPLE ATTRACTORS AND LONG TRANSIENTS IN SPATIALLY STRUCTURED POPULATIONS WITH AN ALLEE EFFECT

I. Vorkamp, S.J. Schreiber, A. Hastings, F.M. Hilker

ABSTRACT

We present a discrete-time model of a spatially structured population and explore the effects of coupling when the local dynamics contain a strong Allee effect and over-compensation. While an isolated population can exhibit only bistability and essential extinction, a spatially structured population can exhibit numerous coexisting attractors. We identify mechanisms and parameter ranges that can protect the spatially structured population from essential extinction, whereas it is inevitable in the local system. In the case of weak coupling, a state where one subpopulation density lies above and the other one below the Allee threshold can prevent essential extinction. Strong coupling, on the other hand, enables both populations to persist above the Allee threshold when dynamics are (approximately) out-of-phase. In both cases, attractors have fractal basin boundaries. Outside of these parameter ranges, dispersal was not found to prevent essential extinction. We also demonstrate how spatial structure can lead to long transients of persistence before the population goes extinct.

3.1 INTRODUCTION

One of the simplest systems with the potential to exhibit a regime shift is a population with a strong Allee effect (Johnson and Hastings, 2018). Population densities above a certain threshold, called Allee threshold, persist whereas populations that fall under the Allee threshold go extinct (Courchamp et al., 2008). There is abundant evidence that Allee effects play an important role in diverse biological systems (Courchamp et al., 2008, 1999; Dennis, 1989; Stephens and Sutherland, 1999; Stephens et al., 1999). Mechanisms that induce an Allee effect, like mate finding problems or defence against predators in small populations, are well understood (Courchamp et al., 2008).

Introducing spatial structure into population models can change their dynamical behaviour. This is of particular relevance when the local dynamics include a strong Allee effect. However, Allee effects were considered mostly in models for spatially structured populations in continuous time (Amarasekare, 1998; Gruntfest et al., 1997; Gyllenberg et al., 1999; Johnson and Hastings, 2018; Kang and Lanchier, 2011; Wang, 2016). One important result from these models is the rescue effect, where a subpopulation that falls under the Allee threshold is rescued from extinction by migration from another location (Brown and Kodric-Brown, 1977). Moreover, Amarasekare, 1998 suggests that local

populations that are linked by dispersal are more abundant and less susceptible to extinction than isolated populations. Little attention has been devoted to the case in discrete time where local dynamics can be chaotic. In that case, the correlation between abundance and extinction risk is less obvious. There have been several studies to understand mechanisms and consequences of coupling patches in discrete time (Earn et al., 2000; Faure, Schreiber, et al., 2014; Franco and Ruiz-Herrera, 2015; Gyllenberg et al., 1996, 1993; Hastings, 1993; Kendall and Fox, 1998; Lloyd, 1995; Yakubu, 2008; Yakubu and Castillo-Chavez, 2002). A controversial question is whether chaotic behaviour of the population increases the probability of extinction (Berryman and Millstein, 1989; Lloyd, 1995; Thomas et al., 1980) or promotes spatially structured populations (Allen et al., 1993) and population persistence (Huisman and Weissing, 1999), which demands further research on coupled patches of chaotic dynamics.

Neubert, 1997 and Schreiber, 2003 study single species models with overcompensating density dependence and Allee effect. Overcompensation occurs as a lagged effect of density-dependent feedback. As a result, populations can alternate from high to low numbers even in the absence of stochasticity (Ranta et al., 2005). This can lead to essential extinction, a phenomenon that does not occur in corresponding continuous-time models. A major characteristic is that large population densities fall below the Allee threshold when the overcompensating response is too strong. Thus, “almost every” initial density leads to extinction when per capita growth is sufficiently high. In that case, Schreiber, 2003 proved that long transient behaviour can occur before the population finally goes extinct. However, an interesting question that has not been studied yet is how the dynamics change when we include spatial structure. In this paper we examine the interplay between essential extinction due to local chaotic dynamics with Allee effect and the between-patch effects due to coupling.

We distinguish two drivers of multistability. Firstly, different states can be caused by the Allee effect (Amarasekare, 1998; Courchamp et al., 1999; Dennis, 1989; Gruntfest et al., 1997; Gyllenberg et al., 1999; Schreiber, 2003). These also exist in isolated patches unless there is essential extinction. Secondly, multistability can be caused by coupling maps with overcompensation (Allen et al., 1993; Gyllenberg et al., 1993; Hastings, 1993; Kendall and Fox, 1998; Lloyd, 1995; Wysham and Hastings, 2008; Yakubu, 2008; Yakubu and Castillo-Chavez, 2002). The former occur also in continuous-time models with Allee effect, while the latter occur in discrete-time overcompensatory models without Allee effect. By including discrete-time overcompensation and Allee effects, we help to unify these separate areas of prior work.

The remainder of the paper is organized as follows. In Section 3.2, we present an overview of the model and our main assumptions. With the aid of numerical simulations, we describe the variety of possible attractors in Section 3.3. Furthermore, we identify conditions under which coupling can prevent essential extinction. We demonstrate two mechanisms by which the whole population can persist, whereas both subpopulations would undergo (essential) extinction without dispersal. Finally, we point out the special role of transients and crises in this model. We conclude with a discussion of the results in Section 3.4.

3.2 MODEL

We consider a spatially structured population model of a single species in discrete time. We assume that at each time step dispersal occurs after reproduction (Hastings, 1993; Lloyd, 1995). The order of events, since there are only two, does not affect the dynamics.

3.2.1 Reproduction (Local dynamics)

The local dynamics are defined by the Ricker map (Ricker, 1954) combined with positive density dependence by an Allee effect. One way to model this is

$$f(x_t) = x_t e^{r(1-\frac{x_t}{K})(\frac{x_t}{A}-1)}, \quad (3.1)$$

where x_t is the population density at time step t and $f(x_t)$ is the population production. Parameters r , K and A describe the intrinsic per-capita growth, the carrying capacity and the Allee threshold, respectively, $r > 0$ and $0 < A < K$.

Applications of this model can be found, for instance, in fisheries or insect models (Estay et al., 2014; Turchin, 1990; Walters and Hilborn, 1976). While this model is not intended to be a realistic representation of a particular species (Neubert, 1997), it captures the main biological features of interest, i.e. the Allee effect and overcompensation. As such, our model formulation, similar to Schreiber (2003), satisfies the following properties:

- There is a unique positive density D that leads to the maximum population density M in the next generation
- Extremely large population densities lead to extremely small population densities in the next generation
- Populations under the Allee threshold A will go extinct

These conditions also hold for other models of that type, e.g. the logistic map with Allee effect or a harvesting term.

Our form of f is chosen in such a way that the Allee threshold is at a fixed value. Other formulations which are based on biological mechanisms (Courchamp et al., 2008; Schreiber, 2003) may be more realistic but make visualization more difficult. However, our results do not depend on this choice.

3.2.2 Dispersal (Between-patch dynamics)

We consider two patches with population densities x_t and y_t at time t . In each patch, we assume the same reproduction dynamics as in Equation (3.1). The patches are linked by dispersal:

$$\begin{aligned} x_{t+1} &= (1-d)f(x_t) + df(y_t), \\ y_{t+1} &= (1-d)f(y_t) + df(x_t), \end{aligned} \quad (3.2)$$

where $d \in [0, 0.5]$ is the fraction of dispersers (0.5 corresponds to complete mixing). Note that apart from initial conditions, the two patches are identical. The state space for this two-patch system is the non-negative cone $C = [0, \infty)^2$ of \mathbb{R}^2 . The solutions of (2.1) correspond to iterating the map $F : C \rightarrow C$ given by $F(x, y) = ((1 - d)f(x) + df(y), df(x) + (1 - d)f(y))$.

3.3 RESULTS

3.3.1 Dynamics without dispersal

In this section, we recap results from the local dynamics which are qualitatively similar to Schreiber, 2003. System (3.1) has three equilibria, $x_1^* = 0$, $x_2^* = A$ and $x_3^* = K$. We distinguish two dynamical patterns for the local case, depending on the threshold value r_{th} that fulfills the equation $f(f(D)) = A$. For $0 < r < r_{th}$ the system is bistable. There is an upper bound \bar{A} with $f(\bar{A}) = A$. For initial densities $A < x_0 < \bar{A}$, the population persists and goes extinct otherwise. The extinction attractor x_1^* is always stable whereas the persistence attractor can be:

- A fixed point/an equilibrium for which $x_t = f(x_t)$;
- A periodic orbit¹ for which $x_t = f^n(x_t)$ but $x_t \neq f^j(x_t) \forall j = 1, \dots, n - 1$; or
- A chaotic attractor (see Broer and Takens, 2010, for a definition).

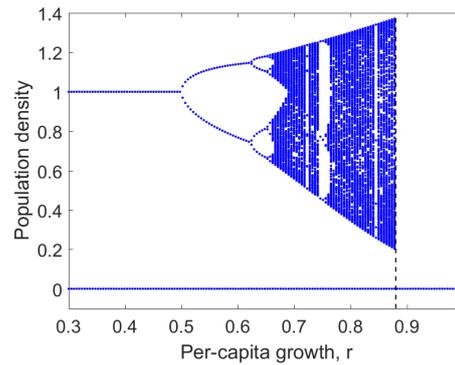
It loses its stability when $r > r_{th}$ and almost every initial density leads to essential extinction, i.e. for a randomly chosen initial condition with respect to a continuous distribution, extinction occurs with probability one (Schreiber, 2003). This is shown in a bifurcation diagram with respect to r in Figure 3.1a. The threshold r_{th} is marked with a dashed line. These properties of the local dynamics (3.1) can be formalized in a Theorem (see Appendix 3.A).

Before turning towards the coupled model we consider two isolated patches, that is System (3.2) and $d = 0$. For relatively small values of r the persistence attractor of f is a fixed point. The combination of equilibria of System (3.1) delivers the equilibria of the uncoupled System (3.2): $(0, 0)$, $(K, 0)$, $(0, K)$, (K, K) , $(A, 0)$, $(0, A)$, (A, A) , (K, A) and (A, K) . Similar to Amarasekare, 1998, the last five equilibria are unstable. The first four equilibria are stable. However, for larger values of r , the persistence attractor is not necessarily a fixed point and can be periodic or chaotic. When it has a linearly stable periodic orbit $\{p, f(p), \dots, f^{n-1}(p)\}$ of period $n \geq 1$, the uncoupled map has $n + 3$ stable periodic orbits given by the forward orbits of the following periodic points

$$\mathcal{P} = \{(0, 0), (0, p), (p, 0), (p, p), (p, f(p)), \dots, (p, f^{n-1}(p))\}. \quad (3.1)$$

For the biological interpretation of the model it is important to note that one can obtain either global extinction of the whole population or persistence above the Allee threshold in one or both patches in the long term. The outcome follows from the dynamical behaviour of the local system. That changes with the introduction of dispersal. Attractors

¹ Note that a fixed point is a periodic orbit of period one.



(a) Local dynamics

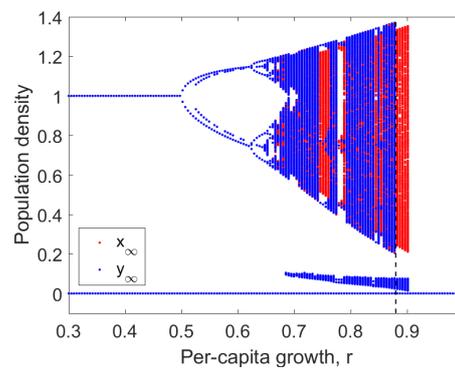
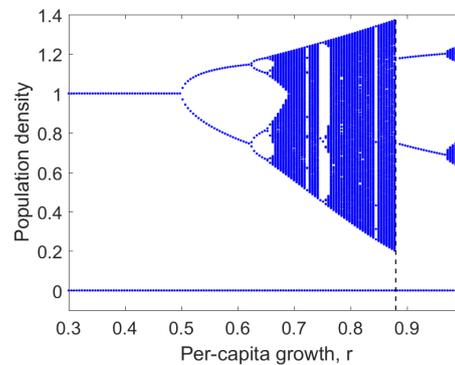
(b) Coupled system $d = 0.03$ (c) Coupled system $d = 0.24$

Figure 3.1: Bifurcation diagram with bifurcation parameter r of (a) the dynamics of a single isolated population and of two populations in the coupled system with (b) dispersal fraction $d = 0.03$ whereby x_∞ (red) is hidden partially by y_∞ (blue) and (c) $d = 0.24$ whereby $x_\infty = y_\infty$, thus only one patch is visible. The essential extinction threshold of an isolated population is marked with a dashed vertical line at $r_{th} = 0.88$. Dispersal can prevent extinction for $r > r_{th}$ in (b) and (c). Allee threshold $A = 0.2$, carrying capacity $K = 1$ and 8000 time steps of which the last 300 are plotted. Initial conditions: $(0.08, 0.19)$, $(0.44, 0.14)$, $(0.73, 0.11)$, $(0.76, 0.73)$, $(0.99, 0.17)$ in all simulations.

can appear or disappear and the fact that essential extinction always occurs for $r > r_{th}$ is no longer true.

3.3.2 Additional attractors in the coupled system

When dispersal is weak and there is a stable positive periodic orbit for f , we prove the following theorem that shows that almost every initial condition converges to one of the $n + 3$ stable periodic orbits in \mathcal{P} . Furthermore, if the positive stable periodic orbit of f is not a power of 2, then there are an infinite number of unstable periodic orbits.

Theorem 1. *Assume the one-dimensional map $f(x)$ has a positive, linearly stable periodic orbit, $\{p, f(p), \dots, f^{n-1}(p)\}$, with period $n \geq 1$. Let U be an open neighborhood of $\cup_{i=1}^n (f \times f)^i(\mathcal{P})$. Then for $d > 0$ sufficiently small*

- (i) *System (3.2) has $n + 3$ distinct, linearly stable periodic orbits contained in U . Let G denote the union of these linearly stable periodic orbits.*
- (ii) *$C \setminus B$ has Lebesgue measure zero where $B = \{(x, y) \in C : \lim_{t \rightarrow \infty} \text{dist}(F^t(x, y), G) = 0\}$ is the basin of attraction of G .*
- (iii) *If n is not a power of 2, then $C \setminus B$ contains an infinite number of periodic points.*

A proof of this theorem is given in Appendix 3.B. Since f is known to undergo period doublings until chaos, one can obtain a large number of attractors for weakly coupled maps. However, our numerical results show that for larger $d > 0$, the number of coexisting attractors is smaller than $n + 3$.

Consider System (3.2) with parameter values $r = 0.63$ and $d = 0.01$. This value of r leads to 4-cycles in the uncoupled system. We observe six stable periodic orbits. Time series for different initial conditions are shown in Figure 3.2. The extinction state in both patches is stable (Figure 3.2a). The two attractors in Figure 3.2b and Figure 3.2c show periodic behaviour above the Allee threshold in one patch and below the Allee threshold in the other patch. We call these attractors *asymmetric attractors*.

In contrast to four different 4-cycles for sufficiently small d (Theorem 1), we observe an in-phase 4-cycle (Figure 3.2d) and only one out-of-phase 4-cycle (Figure 3.2e). The other two 4-cycles with $x_t < 1$, $y_t > 1$ and $x_{t+1} > 1$, $y_{t+1} < 1$ are replaced by only one attractor, an out-of-phase 2-cycle (Figure 3.2f). This is an example for a stabilizing effect of dispersal. In the following, we will call all attractors with population densities above the Allee threshold in both patches *symmetric attractors*.

Final-state sensitivity depending on the initial conditions can occur whenever there are several coexisting attractors (Peitgen et al., 2006). The system can exhibit very different dynamic behaviours even if all parameter values are fixed (Lloyd, 1995). In the following sections, we will first categorize attractors in terms of subpopulations being above or below the Allee threshold. Secondly, we take a closer look at different symmetric attractors, like the ones in Figure 3.2d-f.

For the simulations, we normalize the population density relative to the carrying capacity by setting $K = 1$ and fix $A = 0.2$. Then, there are only two remaining param-

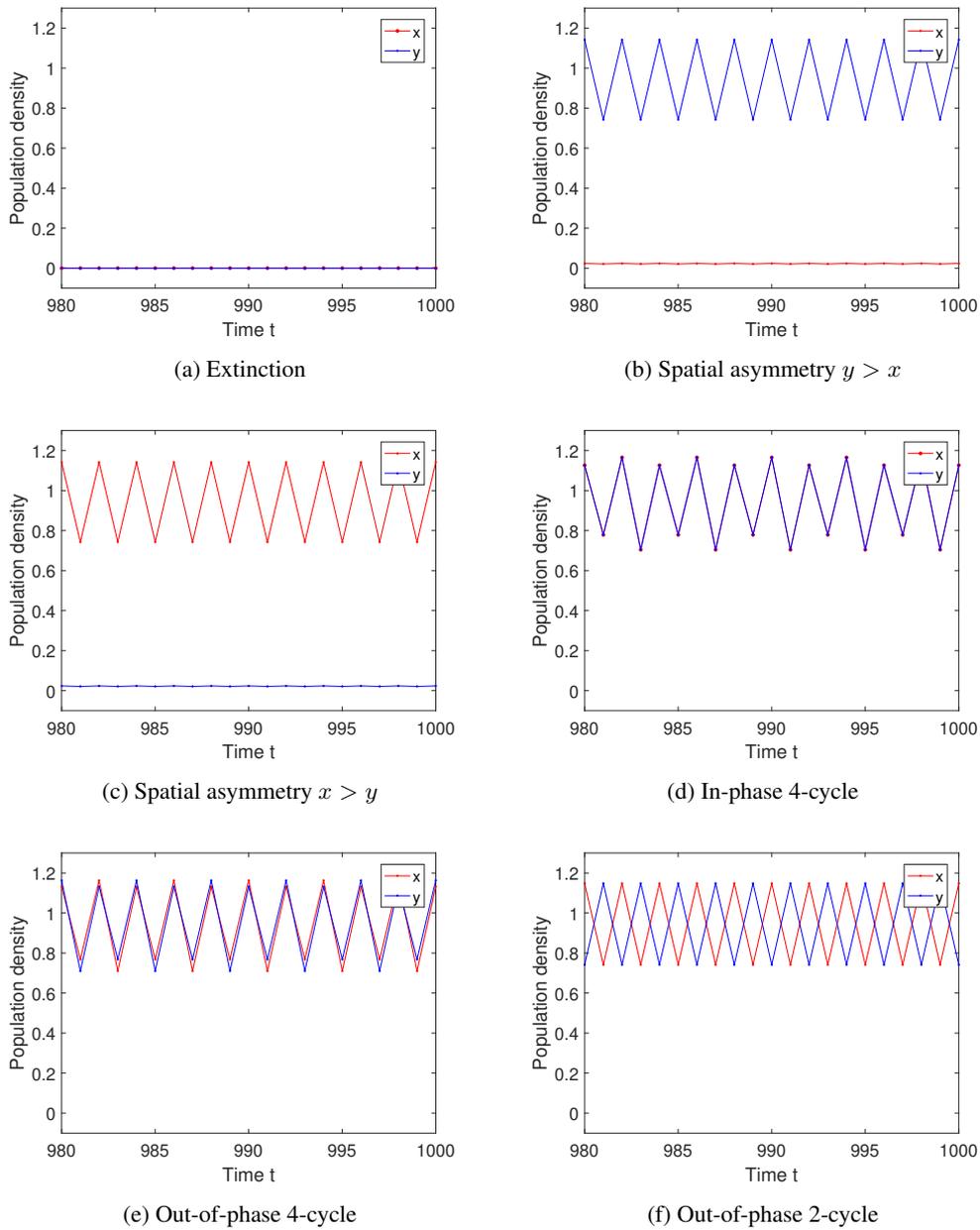


Figure 3.2: Time series of model (3.2) that lead to different attractors because of different initial conditions. Parameters: $K = 1$, $A = 0.2$, $r = 0.63$ and $d = 0.01$. Initial conditions: (a) $x_0 = 0.03$, $y_0 = 0.04$, (b) $x_0 = 0.16$, $y_0 = 0.86$, (c) $x_0 = 0.86$, $y_0 = 0.16$, (d) $x_0 = 0.64$, $y_0 = 0.38$, (e) $x_0 = 0.82$, $y_0 = 0.98$, (f) $x_0 = 0.38$, $y_0 = 0.58$.

eters, r and d . Figure 3.3 summarizes the dynamical behaviour that can be observed in the (r, d) -parameter plane for $0 < d < 0.5$ and $0.3 < r < 1$.

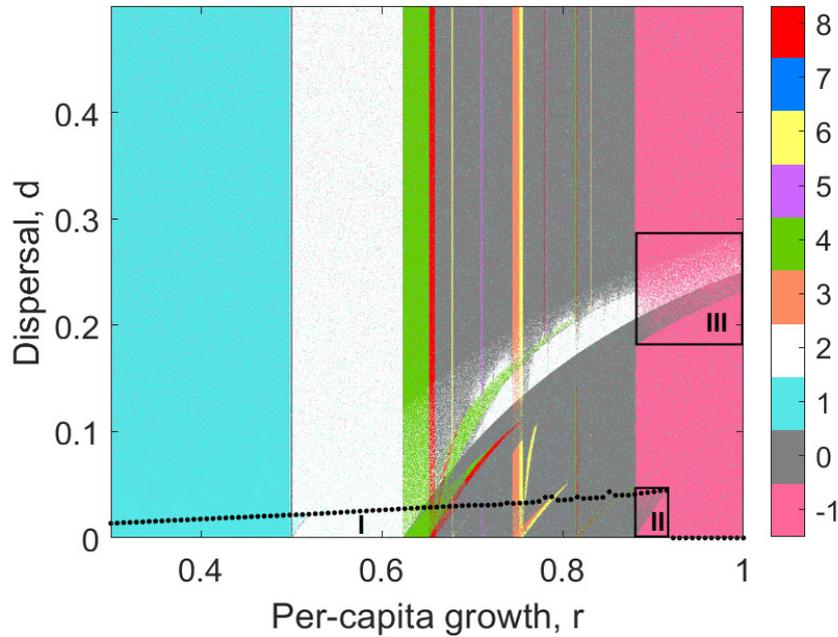


Figure 3.3: Dynamical behaviour characterized by the periodicity, as a function of r and d . Labels of the colour bar give the periodicity of locally stable cycles. Periodicity 1 stands for a stable equilibrium (trivial or non-trivial), 0 for periods > 8 or chaos and -1 for extinction when $A < x_0 < 1 \vee A < y_0 < 1$. Region (I) below the dotted curve indicates for which values of r and d asymmetric attractors appear (tested for 100 random initial conditions) with irregularities due to additional attractors depending on dispersal. Regions (II) and (III) indicate for which values of r and d dispersal can prevent essential extinction. Fuzzy regions indicate multistability. Note that the extinction state is always stable (turquoise sprinkles). $K = 1$ and $A = 0.2$ fixed in all runs. One random initial condition per parameter combination. Selected periodicity has been determined using the *CompDTIME* routine for Matlab (<https://www.imath.kiev.ua/~nastyap/compdtime.html>), provided there was no essential extinction.

3.3.2.1 Multiple attractors due to the Allee effect

In the case of weak dispersal (see Figure 3.3, parameter region I, below dotted curve), the equilibria of the coupled system are similar to the ones of the uncoupled system. This follows from a perturbation argument, similar to Karlin and McGregor, 1972. We observe four attractors that differ in whether the population density in each patch is above or below the Allee threshold. The extinction state $(0, 0)$ is always stable. The two asymmetric and the symmetric attractors can be either equilibria or show periodic/chaotic behaviour, depending on the values of r and d (see Figure 3.3). Thus, spatial asymmetry can be conserved. Figure 3.1b shows the four states in patch y for $d = 0.03$ (blue): when both subpopulations start above the Allee threshold, the population densities remain at carrying capacity K or after period doublings on a periodic/chaotic attractor. If the initial population in patch y is smaller than A but larger in patch x , one

asymmetric attractor is approached (red: large x , blue: small y). If initial populations in both patches are smaller than A , the extinction attractor is approached.

The situation changes for larger dispersal (see Figure 3.3, above dotted curve). The asymmetric attractors disappear and only extinction or persistence above the Allee threshold in both patches is possible. This can be seen in Figure 3.1c, where in comparison to Figure 3.1b no asymmetric attractor is visible.

A nullcline analysis can give information about the number of equilibria that can lead to different attractors. For that, we refer to Amarasekare, 1998 or Kang and Lanchier, 2011, who did a detailed nullcline analysis for a corresponding continuous-time model.

3.3.2.2 *Multiple attractors due to overcompensation*

Multiple attractors can not only appear due to Allee effects but also in coupled maps with overcompensation (Hastings, 1993). Thus, we take a closer look at additional symmetric attractors as shown in Figure 3.2d-f. The in-phase 4-cycle, the out-of-phase 4-cycle and the out-of-phase 2-cycle can coexist even without additional equilibria.

The (r, d) -parameter plane in Figure 3.3 provides some insights for which parameter combinations multiple symmetric attractors appear (Note that in this Figure, we do not distinguish between different attractors of the same period for better clarity): On the one hand, the equilibrium (K, K) undergoes several period-doublings up to chaos and finally essential extinction when increasing r , independently of dispersal (vertical stripe structure). The bending stripes across the diagram, on the other hand, indicate additional attractors depending on both r and d . Fuzzy regions appear when multiple symmetric attractors coexist. Coexisting symmetric attractors can be also seen in Figure 3.1b for $0.5 < r < 0.65$ where in-phase and out-of-phase 2-cycles coexist.

This phenomenon is well understood in models without an Allee effect (Hastings, 1993; Wysham and Hastings, 2008; Yakubu, 2008; Yakubu and Castillo-Chavez, 2002). As it only occurs for the symmetric attractor, where we observe population densities above the Allee threshold, the Allee effect itself is negligible concerning the origins of the non-equilibrium attractors. However, it is important to mention here, since any of the coexisting attractors can disappear due to the Allee effect with the system then collapsing to the extinction attractor. This will be discussed in Sections 3.3.3 and 3.3.4.

Combining the results of discrete-time models with overcompensation (Hastings, 1993; Kendall and Fox, 1998; Lloyd, 1995) and continuous-time models for spatially structured populations with Allee effect (Amarasekare, 1998) shows that the variety of both is expressed here.

3.3.3 *Dispersal induced prevention of essential extinction*

In Section 3.3.1 we have seen that for per-capita growth exceeding the threshold r_{th} isolated populations undergo essential extinction. We now investigate mechanisms that allow “dispersal induced prevention of essential extinction” (DIPEE) in the coupled maps. We choose the parameters such that without dispersal the whole population would go extinct ($r > r_{th}$). We identify two mechanisms for DIPEE: Spatial asymmetry and stabilizing (approximately) out-of-phase dynamics.

3.3.3.1 *DIPEE due to spatial asymmetry*

For the moment, we only consider small dispersal $d < 0.05$ (see Figure 3.3, parameter region II). In this case, the coupling is sufficiently weak to observe different dynamics in both patches. Figure 3.4a, 3.4c and 3.4e show the phase planes with nullclines² and sample orbits for different values of r . In Figure 3.4a all orbits with initial conditions $(A, A) < (x_0, y_0) < (\bar{A}, \bar{A})$ remain on the chaotic symmetric attractor. When r exceeds r_{th} , the symmetric attractor collides with the unstable equilibrium (A, A) and disappears whereas the asymmetric attractors persist. Grebogi et al., 1982 and Bischi et al., 2016 call that phenomenon a boundary crisis. Figure 3.4c presents three cases of orbits with $(A, A) < (x_0, y_0) < (\bar{A}, \bar{A})$: either the whole population goes extinct (dark blue) or the population in one patch drops under the Allee threshold, while the population in the other patch remains above (light blue, green). In this situation, essential extinction can be prevented, depending on the initial conditions. One subpopulation overshoots the equilibrium beyond some critical value (e.g. in patch x) and then drops below the Allee threshold whereas the other subpopulation (e.g. patch y) remains above. This leads to high net dispersal from patch y to patch x . Thus, in patch y , the maximum population density is reduced, so that $f(M) > A$ and essential extinction does not take place. Patch x is rescued from extinction by continual migration from patch y .

The basins of attraction change when r exceeds r_{th} . For $r < r_{th}$ the basins are sharply separated sets as shown in Figure 3.4b. When the symmetric attractor disappears its basin results in a fractal structure (see Figure 3.4d). When parameter r is increased further, DIPEE is not possible. The two asymmetric attractors disappear after another boundary crisis with equilibria near $(0, A)$ and $(A, 0)$ (see Figure 3.4e). Almost all initial conditions lead to the only remaining attractor, the extinction state (see Figure 3.4f).

In summary, for per-capita growth above the local essential extinction threshold r_{th} small dispersal can have a stabilizing effect in terms of reducing the maximum population density and thus preventing essential extinction (see Figure 3.3, parameter region II). This result is emphasized by Figure 3.1b. The asymmetric attractor in which patch y remains below and x above the Allee threshold can persist for values of $r > r_{th}$. Conversely, one can observe the symmetric attractor to disappear at r_{th} . Note that the opposite case in which patch x is below A also persists for $r > r_{th}$ but is not shown in Figure 3.1b.

3.3.3.2 *DIPEE due to stabilizing (approximately) out-of-phase dynamics*

A second mechanism that can prevent essential extinction operates at larger dispersal fractions around $0.19 < d < 0.28$ (see Figure 3.3, parameter region III). In this parameter region, asymmetric attractors are impossible. Both subpopulations either persist above the Allee threshold or go extinct. The extinction state $(0, 0)$ is stable whereas the symmetric attractor shows (approximately) out-of-phase dynamics where both population densities are above the Allee threshold but alternating (see Figure 3.5a). For values $r < r_{th}$, the symmetric out-of-phase dynamics coexist with a chaotic rhombus³. Initial

² The x -nullcline is the set of points satisfying $x_{t+1} = x_t$, cf. Kaplan and Glass, 1998. Similarly, the y -nullcline satisfies $y_{t+1} = y_t$

³ no obvious relationship between x_t and y_t (Kendall and Fox, 1998); the attractor forms a rhombic structure

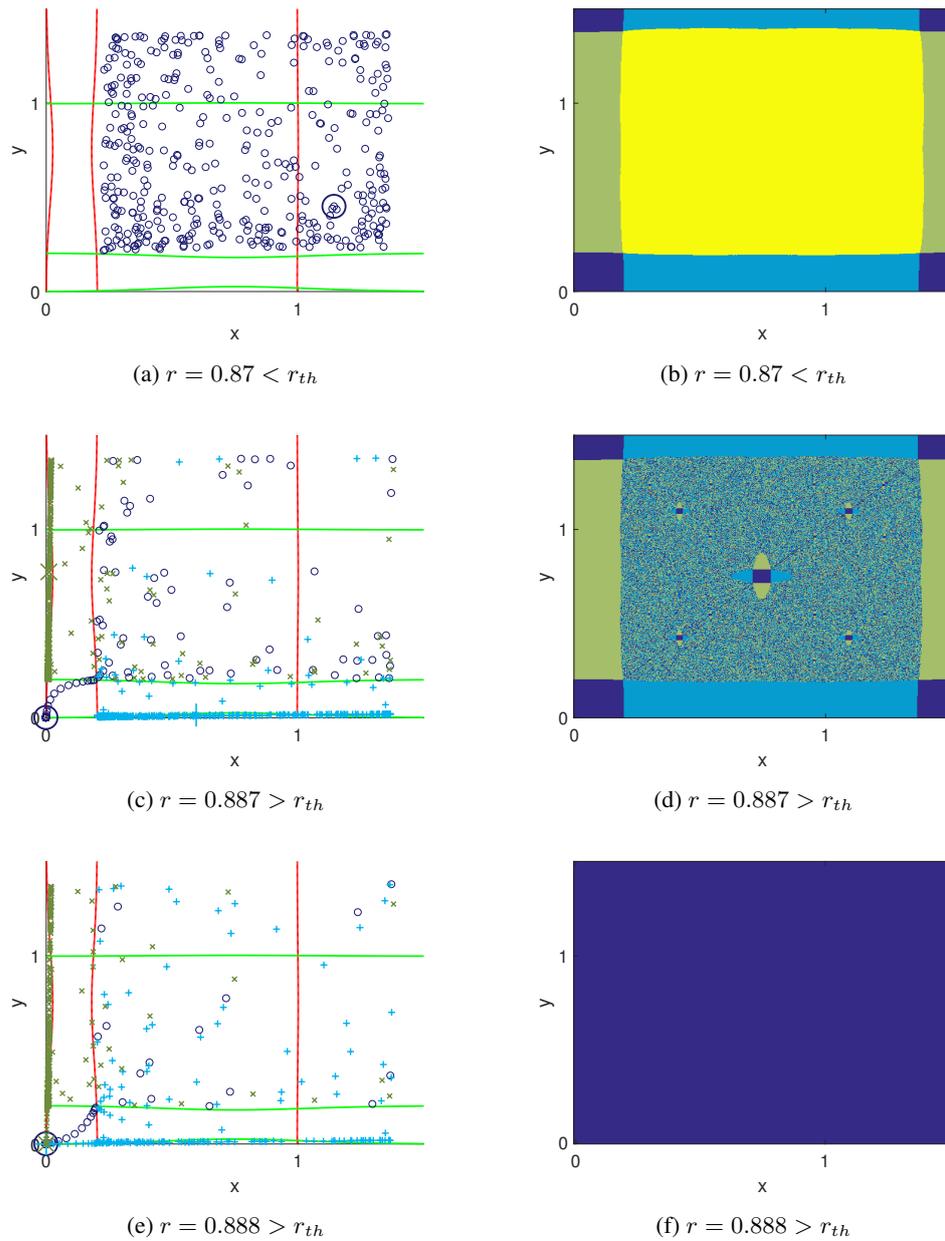


Figure 3.4: Phase planes (left column) and basins of attraction (right column) of the coupled system with $d = 0.01$ and (a,b) $r = 0.87$, (c,d) $r = 0.887$ and (e,f) $r = 0.888$. In the phase planes, sample orbits for initial conditions $(A, A) < (x_0, y_0) < (\bar{A}, \bar{A})$ are shown with dots/crosses. When $r < r_{th}$ the population persists (a). For r exceeding r_{th} two asymmetric states (and thus DIPEE) and the extinction state are possible (c). For sufficiently large r extinction is inevitable (e). Large symbols mark the final states. Nullclines in red and green, respectively. Basins of attraction of the four attractors in panels (b), (d) and (f): Extinction (dark blue), asymmetric coexistence (light blue and green), symmetric coexistence (yellow). Clear basin boundaries (b), fractal basin boundaries between asymmetric coexistence and extinction (d) or no boundaries (f) depending on the value of r . Allee threshold $A = 0.2$, carrying capacity $K = 1$ and 2000 time steps in all simulations.

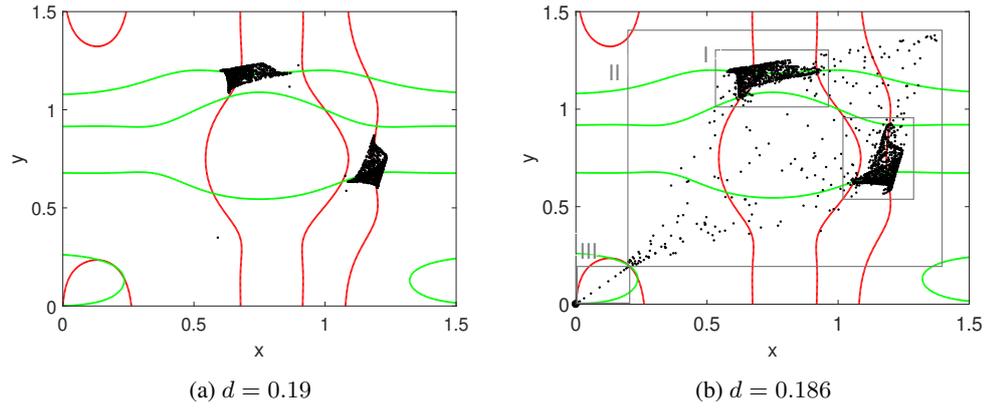


Figure 3.5: Phase planes with nullclines of the second iteration of System (3.2) with $r = 0.89$ and (a) $d = 0.19$ and (b) $d = 0.186$. The approximately out-of-phase attractor (a) undergoes a boundary crisis (b, region I). The emerging chaotic rhombus (b, region II) again merges the unstable equilibrium (A, A) and finally converges to the extinction state (b, region III). Allee threshold $\bar{A} = 0.2$, carrying capacity $K = 1$, $(A, A) < (x_0, y_0) < (\bar{A}, \bar{A})$, 1000 time steps, large symbol: final state.

conditions $(A, A) < (x_0, y_0) < (\bar{A}, \bar{A})$ lead either to one or the other attractor. When r exceeds r_{th} , the chaotic rhombus collides with the unstable equilibrium (A, A) (similar to Figure 3.7) and disappears whereas the (approximately) out-of-phase dynamics persists. Figure 3.1c shows the drastic change of possible attractors at r_{th} . In one time step more individuals move from patch x to y . In the next step, net movement is from y to x so that values in the two patches cover the same range. Thus, only one patch is visible in Figure 3.1c. The other patch is overlaid completely. The antagonistic net movement prevents an overshoot in both patches and both are rescued from essential extinction. Again, one should note that DIPEE is very sensitive to the choice of initial conditions. More precisely, different initial conditions $(A, A) < (x_0, y_0) < (\bar{A}, \bar{A})$ lead either to synchronization and thus essential extinction or to coexistence with population densities above the Allee threshold in both patches and thus DIPEE.

Also the basins of attraction change when r exceeds r_{th} . For $r < r_{th}$ the basins are sharply separated sets as shown in Figure 3.6a. When the chaotic rhombus disappears the basins of attraction for symmetric attractors split into a fractal structure (see Figure 3.6b). This structure is well known from other studies on coupled maps with local overcompensation (Gyllenberg et al., 1993; Hastings, 1993; Lloyd, 1995). The significant difference here is that attractors are distinguished not in their period but in the sense that slightly different initial conditions lead either to survival or to extinction. From the ecological point of view, that is a crucial difference.

3.3.3.3 No DIPEE

For $0.05 < d < 0.19$ and $d > 0.28$, dispersal can not prevent essential extinction (see Figure 3.3, $r > r_{th}$, outside of regions II and III, pink parameter region). The symmetric attractor is a chaotic rhombus (see Figure 3.7a) which disappears after a

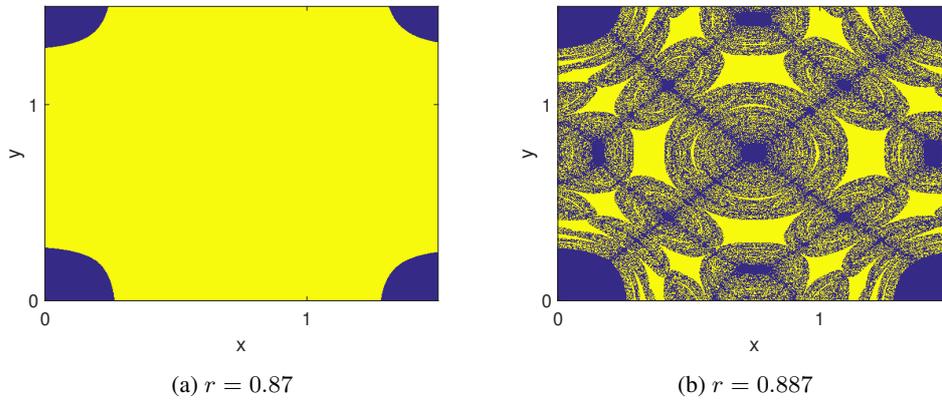


Figure 3.6: Basins of attraction for $d = 0.23$ and (a) $r = 0.87$ and (b) $r = 0.887$. Blue indicates the extinction state whereas yellow marks symmetric coexistence attractors. When r exceeds r_{th} , the basins change to a fractal structure. Allee threshold $A = 0.2$, carrying capacity $K = 1$ and 1000 time steps in all simulations.

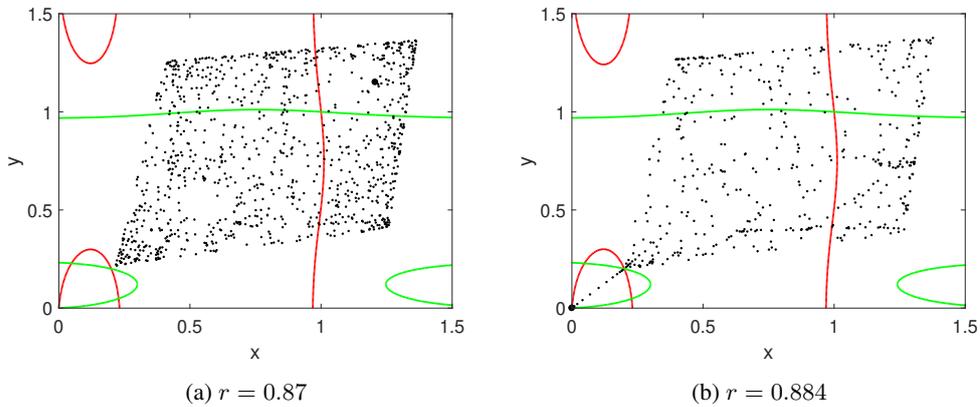


Figure 3.7: Phase planes of the coupled system with $d = 0.1$ and (a) $r = 0.87$ and (b) $r = 0.884$, between which a boundary crisis eliminates the symmetric coexistence attractor. Allee threshold $A = 0.2$, carrying capacity $K = 1$, $(A, A) < (x_0, y_0) < (\bar{A}, \bar{A})$, 1000 time steps in both simulations, large symbols: final state. Nullclines in red and green, respectively.

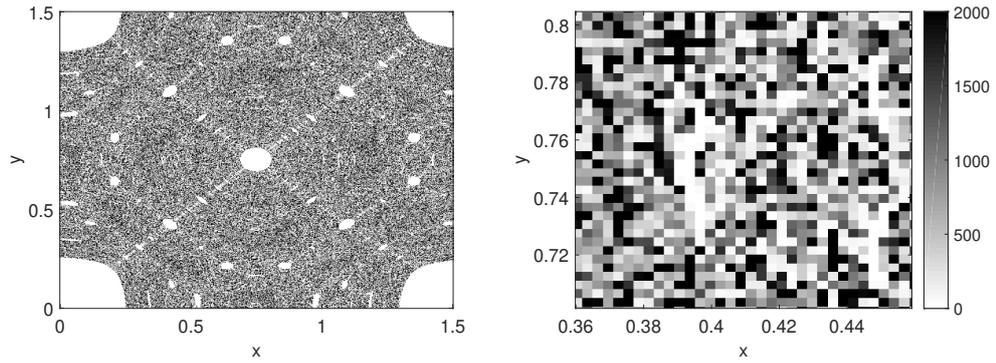


Figure 3.8: Left: time to extinction for parameter values $r = 0.89$, $d = 0.186$ and initial conditions $x_0, y_0 \in (0, 1.5)$. Grey scale is chosen such that white means extinction after few time steps $t \approx 0$ and black means extinction at $t \approx 2000$ or later (see color bar). The population is called extinct at time t when $x_t + y_t < 10^{-4}$. Right: enlarged section for selected initial conditions x_0, y_0 .

boundary crisis for $r > r_{th}$ and thus leads to essential extinction for almost all initial conditions (see Figure 3.7b).

3.3.4 Transients and crises

Transients are the part of the orbit from initial condition to the attractor and of particular importance in the case of crises (Hastings et al., 2018). A boundary crisis occurs when an attractor exceeds the basin boundary around an invariant set, e.g. an equilibrium or a cycle (Bischi et al., 2016; Hastings et al., 2018; Neubert, 1997; Vandermeer and Yodzis, 1999; Wysham and Hastings, 2008). Then the previous attractor forms a chaotic repeller or saddle and leads to long transients (Schreiber, 2003; Wysham and Hastings, 2008). Schreiber, 2003 found long transients in a corresponding local model in parameter regions of essential extinction and proved that the time to extinction is sensitive to initial conditions due to the chaotic repeller formed by the basin boundary collision. The transient behaviour which is seen in Figures 3.4, 3.5 and 3.7 can be partially explained with knowledge of the local system. We can also identify long transients induced by chaotic repellers or saddles. However, the coexistence of different persistence attractors can lead to different transient stages or transients that last orders of magnitudes longer than in the local case. In the following, we give numerical examples for both.

Different stages of transients before extinction of the population are shown in Figure 3.5. The approximately out-of-phase attractor (I) in Figure 3.5a undergoes a boundary crisis when d decreases and merges with the transient chaotic rhombus that is also seen in Figure 3.7b. The two attractors disappear but are visible as ghosts (Figure 3.5b, I and II). Finally the population goes extinct (Figure 3.5b, III). In contrast to Figures 3.4 and 3.7, the nullclines of the second iteration⁴ in Figure 3.5 highlight the invariant set at which the boundary crisis occurs (intersections of green and red nullclines). Figure 3.8 presents the time to extinction for a range of initial population densities and the same

⁴ The nullclines of the second iteration are the set of points satisfying $x_{t+2} = x_t$ for population x and $y_{t+2} = y_t$ for population y , respectively (cf. Kaplan and Glass, 1998).

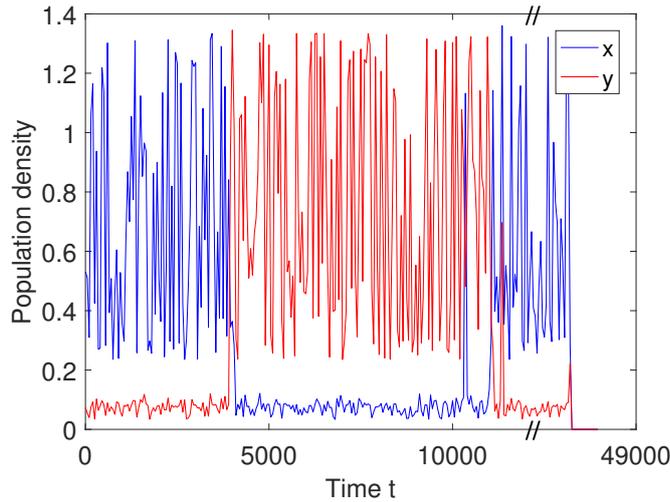


Figure 3.9: Time series for parameter values $r = 0.898$, $d = 0.0415$ and initial conditions $x_0, y_0 = (0.07381, 0.53102)$. Time steps $t \in (12000, 45000)$ are hidden by a broken x-axis. Only every fifth value is plotted for better clarity.

parameters as used for Figure 3.5b. The sensitivity to initial conditions of transients is similar to the local system. The range of times until the population goes extinct reaches from values ≈ 0 to more than 2000 time steps (Figure 3.8). A steady-state analysis would not provide this information. From an ecological perspective, it is often more important to understand the transient than the asymptotic behaviour since this is on the relevant time scale. In contrast to regime shifts, where small parameter changes can lead to huge changes in the systems state, transient shifts can occur without additional environmental perturbations.

Figure 3.9 shows a case of extremely long transients (Hastings et al., 2018). The system passes the first 4700 time steps on one asymmetric ghost attractor until it switches to the other asymmetric ghost for the following 6000 time steps. Then the system switches back to the former ghost attractor, a behaviour that occurs due to a crisis in this parameter region. The long transient of about 34000 time steps ends abruptly and the population goes extinct after more than 46000 time steps without any parameter changes.

3.4 DISCUSSION AND CONCLUSIONS

In this paper, we have developed a model for a spatially structured population with a local Allee effect and overcompensation. We found attractors to appear and disappear in the presence of dispersal. In contrast to Knipf and Röst, 2016 who state that the situation simplifies when dispersal increases, this conclusion does not hold for the model presented here. Nevertheless our results confirm two lines of research. Following Amarasekare, 1998, we showed that populations in patchy environments can have a large number of equilibria if both positive and negative density dependence are considered. We categorized extinction, symmetric and asymmetric attractors. Secondly, we identified additional symmetric attractors, analogous to Hastings, 1993. However, by

Theorem 1 we gave conditions under which the behaviour of the coupled system can be derived from the behaviour of the uncoupled map. Overall, this simple model shows the complexity of interaction between chaotic dynamics, the Allee effect and dispersal. In contrast to continuous-time models that suggest populations that are linked by dispersal to be more abundant and hence less susceptible to extinction (Amarasekare, 1998), in discrete-time models not only small populations are endangered. However, we found two mechanisms that can prevent essential extinction of a spatially structured population whereas it takes place in the corresponding uncoupled system. Weak coupling of the two maps allows spatial asymmetry. Hence, it is possible to find one subpopulation with density above and one below the Allee threshold also for per-capita growth that leads to (essential) extinction without dispersal. Stronger coupling allows both subpopulations to persist above the Allee threshold due to (approximately) out-of-phase dynamics. Outside these parameter regions dispersal provides no mechanism to prevent essential extinction and the population goes extinct in almost all cases.

In summary, we support the conclusion of Amarasekare, 1998 that interactions between Allee dynamics and dispersal create between-patch effects that lead to qualitative changes in the system. Populations are able to persist below the Allee threshold (rescue effect). Moreover, DIPEE provides another rescue effect for populations that suffer from essential extinction. The population with density below the Allee threshold is rescued from extinction and the population with density above the Allee threshold is rescued from essential extinction. Both subpopulations are prone to extinction without dispersal. However, a possibility for DIPEE is given only for specific initial conditions with a fractal basin boundary. For instance, DIPEE due to approximately out-of-phase dynamics for high dispersal benefits from asynchronous behaviour in the two patches (Lloyd, 1995). Small perturbations can synchronize this strongly connected system and thus lead to extinction (Earn et al., 2000).

Finally, we demonstrated the importance of the time scale since boundary crises may lead to long transients. Transient behaviour occurred also in the corresponding local system (Schreiber, 2003). Our results for the coupled system support the statement that chaotic transients can last hundreds of time steps before the extinction state is reached. The duration of transients is also found to be sensitive to initial conditions. However, with the spatial structure of the model in this study, different persistence attractors can coexist. These can lead to different transient stages or transients that last orders of magnitudes longer than in the local case. A steady-state analysis will give no information about how long it takes a population to go extinct and what happens until extinction. On the other hand, short time series will eventually conceal that a population is damned to extinction for given parameters. Thus, a comprehensive analysis is fundamental to understand the complex behaviour of the presented system. This statement is supported for instance by Wysham and Hastings, 2008 or Hastings et al., 2018 who point out that ecologically relevant time scales are typically not the asymptotic time scales. In a next step, the impact of stochastic processes in the model could be tested since they are of particular importance in systems with multistability. Furthermore, a discrete-state model could be studied to investigate how lattice effects which inhibit chaos will lead to different dynamical behaviour (Henson et al., 2001). A question that we also do not address in this paper, is the significance of the chosen number of patches (Allen et al.,

1993; Knipl and Röst, 2016). One could argue that in the case of more patches some effects may get lost or more pronounced. Further studies are needed to investigate the phenomena described (DIPEE, multiple attractors) on a broader spatial scale. Finally, the properties of dispersal could be refined in terms of asymmetric dispersal or dispersal mortality (Amarasekare, 1998; Wu et al., 2020).

Our model formulation is generic and does not depend on the Ricker growth model or the chosen implementation of the Allee effect. It is more about effects that are produced by coupled patches of locally overcompensatory dynamics with an Allee effect (Schreiber, 2003). We tested other models of the same type and got similar results (not presented here). That is in line with Amarasekare, 1998 and Hastings, 1993, who mention the generality of their results.

In summary, this paper contains some interesting results from the ecological and mathematical point of view: One key message is that small changes of parameters, perturbations or environmental conditions can have drastic consequences for a population. Even without external perturbations seemingly safe and unremarkable dynamics (long transients) can abruptly lead to extinction (Hastings et al., 2018). This is of particular importance for species that show chaotic population dynamics. In this case they can be at risk not only for small population densities.

The effect of dispersal and connectivity can be either positive or negative. On the one hand dispersal can mediate local population persistence (rescue effect) or reduce overshoots and thus prevent essential extinction (DIPEE). On the other hand, dispersal can reduce local population sizes under the Allee threshold (Figure 3.3, pink sprinkles in $r < r_{th}$) or induce an overshoot and thus cause (essential) extinction. These negative effects were not investigated in this work but should not be neglected. From the mathematical point of view it is interesting to observe a simple model setup with such a complexity in terms of multiple attractors and surprising results, e.g. long transients, caused by ghost attractors after various boundary crises (Hastings et al., 2018).

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APPENDIX

3.A THEOREM 2

Theorem 2. *Let $f : [0, \infty) \rightarrow [0, \infty)$ be a three times continuous differentiable function that fulfills the following conditions:*

- (i) *f has a unique critical point D*
- (ii) *There exists an interval $[a, b]$ with*
 - (a) *$f(x) > 0 \forall x \in [a, b]$*
 - (b) *There is an $A \in (a, b)$ such that $f(A) = A$ and $f(x) \neq x \forall x \in (0, A)$*
 - (c) *$\lim_{n \rightarrow \infty} f^n(x) = 0 \forall x \notin [a, b]$*
 - (d) *The Schwartzian derivative of f is negative for all $x \in [a, b]$*

Define $A^* = \max\{f^{-1}(A)\}$ and $M = f(D)$. Then:

- **Bistability:** *If $f(M) > A$, then $f^n(x) \geq A \forall n \geq 0, x \in [A, A^*]$ and $\lim_{n \rightarrow \infty} f^n(x) = 0 \forall x \notin [A, A^*]$.*
- **Essential extinction:** *If $f(M) < A$, then $\lim_{n \rightarrow \infty} f^n(x) = 0$ for Lebesgue almost every x .*
- **Chaotic semistability:** *If $f(M) = A$, then the dynamics of f restricted to $[A, A^*]$ are chaotic and $\lim_{n \rightarrow \infty} f^n(x) = 0 \forall x \notin [A, A^*]$.*

According to Schreiber, 2003, we show that the criteria (i) and (ii) hold for function (3.1) with parameter values $K = 1, r > 0$ and $0 < A < K$. That is, (3.1) shows either bistability or essential extinction, depending on the parameter values.

- (i) f has a unique positive critical point D at:

$$x = \frac{1 + A}{4} + \frac{1}{4} \sqrt{\frac{8A + r + 2Ar + A^2r}{r}}$$

- (ii) For an interval $[a, b]$ where $a, b > 0$
 - (a) is fulfilled by the product of two positive values (x itself and the exponential function).
 - (b) is fulfilled by the Allee threshold A . For all $0 < x < A$ we get $f(x) < x$ since the exponential function has a negative exponent and is thus smaller than one.

- (c) Choose $a \in (0, A)$. $\lim_{x \rightarrow \infty} f(x) = 0$ and f has a unique positive critical point. Thus, there exists a unique $b > a$ such that $f(b) = a$. It follows that $f(x) \in [0, A]$ for all $x \in [b, \infty)$. Hence, (c) is fulfilled.
- (d) The Schwartzian derivative of f is:

$$Sf(x) = -\frac{q_1^2(x)q_2(x) + \frac{12r^2x^2}{A^2} + \frac{12r}{A}}{2(1+xq_1)^2}$$

with

$$q_1(x) = r \left(\frac{1-2x}{A} + 1 \right)$$

$$q_2(x) = 6 + x^2 + q_1^2(x) + 4xq_1(x)$$

All terms except $q_2(x)$ are obviously positive. For $q_2(x)$, we have:

- $q_2(0) = 6$
- The only minimum (for positive values of x) occurs at

$$x_{min} = \frac{1+A}{4} + \frac{1}{4} \sqrt{\frac{16A+r+2Ar+A^2r}{r}}$$

with $f(x_{min}) = 2$.

- $\lim_{x \rightarrow \infty} q_2(x) = \infty$.

In summary, q_2 is also positive. Thus, the Schwartzian derivative is negative for all $r > 0$, $A > 0$ and $x > 0$.

3.B PROOF OF THEOREM 1

To prove the theorem, let $\tilde{F}(x, y) = (f(x), f(y))$ denote the uncoupled map and let $F(x, y) = ((1-d)f(x) + df(y), df(x) + (1-d)f(y))$ be the coupled map with $d > 0$. Assume that f has a linearly stable periodic orbit $\mathcal{O} = \{p, f(p), \dots, f^{n-1}(p)\}$ of period n with $p \in [A, \infty)$. Since f has a negative Schwartzian derivative and a single critical point on the interval $[A, \infty)$, Theorem A of Strien (1981) implies that the complement of the basin of attraction of \mathcal{O} for f can be decomposed into a finite number of compact, f -invariant sets which have a dense orbit and are hyperbolic repellers: there exists $c > 0$ and $\lambda > 1$ such that $|(f^t)'(x)| \geq c\lambda^t$ for all points x in the set and $t \geq 1$. Consequently, the 2-dimensional mapping \tilde{F} is an Axiom A endomorphism (Przytycki, 1976, pg. 271): the derivative of \tilde{F} is non-singular for all points in the non-wandering set $\Omega(\tilde{F}) = \{(x, y) \in C : \text{for every neighborhood } U \text{ of } (x, y), \tilde{F}^t(U) \cap U \neq \emptyset \text{ for some } t \geq 1\}$, $\Omega(\tilde{F})$ is a hyperbolic set, and the periodic points are dense in $\Omega(\tilde{F})$. Przytycki (1976, 3.11-3.14 and 3.17) imply that (i) $\Omega(\tilde{F})$ decomposes in a finite number of invariant sets $\Omega^1(\tilde{F}), \dots, \Omega^m(\tilde{F})$ and (ii) maps sufficiently C^1 close to \tilde{F} are Axiom A endomorphisms whose invariant sets $\Omega^i(F)$ are close to $\Omega^i(\tilde{F})$. In particular, property (ii) implies that $F(x)$ is an Axiom A endomorphism provided that $d > 0$ is sufficiently small. The invariant sets $\Omega^i(\tilde{F})$ for \tilde{F} correspond the linearly stable periodic orbits defined by \mathcal{P} , and products of the hyperbolic repellers for f and the linearly stable pe-

riodic orbits of f . Without loss of generality, let $\Omega^i(\tilde{F})$ for $1 \leq i \leq n+3$ correspond to the linearly stable periodic orbits of \tilde{F} and $\Omega^i(\tilde{F})$ for $i > n+3$ correspond to the saddles and repellers of \tilde{F} . For $d > 0$ sufficiently small, $\Omega^i(F)$ retain these properties. For $d \geq 0$ sufficiently small, the proof of Theorem IV.1.2 in Qian et al. (2009) implies that the complement of the basin attraction of $\cup_{i=1}^{n+3} \Omega^i(F)$ has Lebesgue measure zero. To prove assertion (iii), assume n is not a power of 2. Then Sharkovskii (1995) proved that f has an infinite number of periodic orbits. All but two of these periodic orbits lie in the hyperbolic repellers of f . Consequently, the set of saddles and repellers $\cup_{i>n+3} \Omega^i(\tilde{F})$ of \tilde{F} contain an infinite number of periodic points. Hyperbolicity of these saddles and repellers implies that the set of saddles and repellers $\cup_{i>n+3} \Omega^i(F)$ of F has an infinite number of periodic orbits for $d > 0$ sufficiently small.

Part II

COUPLED MODELS: AGRI-ENVIRONMENT SCHEMES
IN AGRICULTURAL LANDSCAPES

FARMERS' LAND-USE DECISION MAKING: A DYNAMICAL MODELLING APPROACH TO INVESTIGATE EFFECTS OF SOCIAL NORMS AND THE POTENTIAL OF INFORMATIVE CAMPAIGNS FOR BIOLOGICAL CONSERVATION

I. Vorkamp, F.M. Hilker

ABSTRACT

1. The concept of the *homo oeconomicus* is often used to model human behaviour in economic contexts. However, other factors like tradition or the preference to comply with social norms can play a role in decision-making processes.
2. To emphasize the need for incorporating non-pecuniary values in economic models, we use data for participation in several agri-environment schemes (AES) in Europe and show that dynamical patterns can not be explained by the *homo oeconomicus* concept. The presented data shows gradually increasing participation levels in AES even if payment levels are constant. Furthermore, low participation levels are sometimes observed despite appropriate for incentive schemes.
3. We propose and investigate a dynamic mathematical model to implement social norms in farmers' land-use decision-making in the face of AES. This socio-economic model can help to explain the discrepancy of predicted and observed behaviour. It can generate multistable dynamics regarding the level of AES participation in the long-term. We further assume that informative campaigns and/or nudging can modify farmers' perception of norms. Campaigns can have a stabilizing effect if strong enough.
4. The attempt of this work is to gain a better understanding of how to model social human behaviour in economic contexts.

4.1 INTRODUCTION

Biodiversity loss is an increasingly pressing problem particularly in agricultural landscapes (Waldron et al., 2017). Agri-environment schemes (AES) aim at biological conservation while keeping the producing role of agriculture in mind (Baylis et al., 2008). Individual contracts for payments are intended to compensate farmers for costs and foregone farming revenue accompanied with a conservation measure (Bateman et al., 2013; Kuhfuss et al., 2016). However, even after decades of a Common Agricultural Policy in the EU, many environmental problems still exist (Henderson et al., 2013; Reimer et al., 2012; Thomas et al., 2019) and many species continue to decline (see, for instance,

insect declines in Germany (Hallmann et al., 2017) or the “Farmland Bird Index” in the UK (Ramírez, 2018)). One potential explanation for the failure of conservation measures is that not enough farmers participate in the AES. In this paper, we address this issue and try to gain a better understanding of why farmers might not participate in AES and which implications that can have for the design of future conservation schemes.

Generally, AES are developed under the *homo oeconomicus* concept, meaning that farmers who are compensated for costs and forgone farming revenue are assumed to implement a conservation measure and thus participate in the scheme. However, Le Coent et al., 2018 report that some farmers are extremely reluctant to switch to new farming practices even when the payment level is above additional costs and income foregone. Furthermore, a large number of studies suggest that income is a significant, but not the only predictor of farmers' land-use decisions. Besides economic factors like the dependency of the household income on farming activity, also non-pecuniary factors like the relationship with neighbouring farmers and their opinion on environmentally friendly practices (social prestige) can play a role (Beedell and Rehman, 1999; Defrancesco et al., 2008; Hynes and Garvey, 2009; Reimer et al., 2012; Sattler and Nagel, 2010; Thomas et al., 2019; Wynne-Jones, 2013). In this work, we focus on non-pecuniary factors that fall under the idea of *social norms* (Elster, 1989). Social norms are behavioural rules supported by a combination of empirical and normative expectations (Thøgersen, 2014). Many examples like littering, smoking or fashion can be found in everyday life (Bicchieri and Mercier, 2014; Bikhchandani et al., 1992; Sunstein, 1996). However, social norms also appear in economic contexts (Nyborg et al., 2006) and could help to explain why the conservation success of AES is still limited (Dessart et al., 2019; Thomas et al., 2019; Willock et al., 1999a). Social norms are well known in the field of behavioural economics but this knowledge is barely used in economic models (e.g. Barraquand and Martinet, 2011).

To strengthen the necessity of a new concept in modelling human behaviour in economic contexts, we make a contribution in this direction by identifying typical dynamical patterns in empirical data of AES participation in Europe. These are, firstly, time delays in behavioural changes of farmers after the start of an AES and, secondly, low participation levels despite appropriate compensation payments. Both prominent patterns can not be explained with classical economic models (Sutherland and Darnhofer, 2012). To that end, we investigate a dynamic mathematical model for the decision-making process of farmers which is influenced by monetary incentives as well as social norms. The effect of social norms in this example is understood as the tendency of a farmer to participate rather in an AES when farmers in the neighbourhood¹ do so (Kuhfuss et al., 2016). Vice versa, a farmer participates less when few neighbors do so. This effect is also known as *descriptive norms* which describe the perception of which behaviour is typically performed by others (Cialdini, 2003).

To reflect social behaviour in models, game-theoretical approaches are often used (Le Coent et al., 2018; Nyborg et al., 2006). The aim is to find *stable* strategies of actors to get information about which behaviour is probably performed (e.g. the voter model). A different approach is to use stochasticity to include social learning such that actors change their behaviour with some probability when being influenced by their social net-

¹ Neighbourhood could be understood not only geographically, but also as social network in this context.

work (Innes et al., 2013). Deterministic models that include bounded rationality in the decision-making rather target questions about common resources (Iwasa et al., 2007; Sun and Hilker, 2020b; Tavoni et al., 2012). In contrast to that, we use the idea of a deterministic utility function to reflect social behaviour in a context with no common resource (Henderson et al., 2013, 2016a). Utility in economics is understood as ranking different situations regarding their desirability. Thus, if a person prefers option one over option two, the utility assigned to option one is higher. Utility can record only the relative desirability, though. The exact value is meaningless (Nicholson and Snyder, 2012). This concept is used in this paper to reflect that a farmer perceives a utility in complying with social norms. Our results show that social norms can help to explain the discrepancy of predicted and real behaviour and that their inclusion in the model leads to a match with the dynamical patterns observed in the empirical data.

Furthermore, we assume that farmers can change their perception and attitude due to information that promotes the AES, e.g. via newsletters, lobbies, professional magazines (Defrancesco et al., 2008; Henderson et al., 2016b; Kuhfuss et al., 2016; Mathijs, 2003; Schultz et al., 2007; Willock et al., 1999a,b). This assumption is based on the *availability heuristic* which states that people tend to overestimate the frequency of events they have encountered recently or frequently (Ajzen, 1996; Tversky and Kahneman, 1973). This form of nudging² is incorporated in our model by a shift of the social utility function. We use this to explain why farmers react differently to schemes with equal compensation level.

4.2 MATERIAL AND METHODS

4.2.1 AES participation in Europe

Two data sets of AES participation in Europe are used to motivate the model presented in this paper. Firstly, we use data of registered organic farms³ in the EU in the period from 1997–2018 (indicator OIH_03 in *CMEF Indicator data*). Since the data is divided into countries, it allows us to compare dynamical patterns of the development of organic farming in the 28 member states. The data needs to be treated with caution, however. EU reforms regarding cross-compliance (2003) and greening-measures (2013) changed the conditions during the time period (Thomas et al., 2019). That might have influenced behavioural patterns. It is also not feasible to assume the same amount of compensation for all farmers for two reasons: firstly, organic farmers have various options to receive subsidies, e.g. for animal welfare, support for areas with natural constraints and aid for marketing and promotion of organic products. Secondly, differences between countries arise since payments are split into support by the EU Common Agricultural Policy and national co-financing (European Commission, 2019).

We distinguish the three categories of temporal developments, namely sudden increases, gradual increases and no clear increases. The classification criteria are set as follows. If the number of participants in a country double within three years after the start or

² Aspect of the choice architecture that alters people's behaviour in a predictable way without forbidding any options or significantly changing their economic incentives (Thaler and Sunstein, 2009)

³ Organic farming is not an AES in the strict sense but administered as one.

a reform of the scheme (which we treat as a start of a new scheme) and stay almost constant otherwise, we consider it a *sudden increase*. If no such marked time period of drastic increase exists but participation numbers grow over time, we consider it a *gradual increase*. All other countries, for which the data shows no or a decreasing trend or only few data points exist, are considered to show *no clear increases* in participation numbers.

The second data set is from the program for agriculture and rural development (PROFIL) in Lower Saxony and Bremen, Germany. The program promoted, inter alia, extensive grasslands in the funding period 2007–2014 (Reiter et al., 2016). The data used in this paper consists of the area (ha), farmers applied for the AES for, corrected by withdrawn areas. PROFIL replaced previous programs for agriculture and rural development in Lower Saxony and Bremen after EU reforms. Thus, as a simplifying assumption, 2007 can be seen as the start of the scheme. Extensive grasslands were promoted twofold under PROFIL. On the one hand, an action-oriented payment B1 compensated farmers when they fulfilled requirements regarding watering, fertilizer usage and the date of first mowing. On the other hand, a results-based payment B2 compensated farmers if they annually proved the presence of four indicator species (Reiter et al., 2016). The payments were, with an amount of 110 €/ha, the same for both schemes. Note that the two data sets are different in what is measured: the first data presents organic operators whereas the second one presents area of land under the AES. For simplicity, we assume that operators participating in an AES and the area they apply for are positively correlated, being aware that farm size and characteristics are highly variable.

4.2.2 Model

We consider a grid of $n \times n$ patches to model a landscape of agricultural fields. Each patch represents a field of 1 ha size and is owned by one farmer. All land-use decisions are assumed to be independent from each other. The land-use decision for a field is based on either solely economic factors or based on a combination of economic factors and social pressure due to descriptive norms. Similar to Allaire et al., 2009, we use the local network of adjacent fields to determine what a farmer perceives as the typically performed behaviour. A conceptual framework of the model is shown in Figure 4.1.

4.2.2.1 Economic assumptions

We follow Barraquand and Martinet, 2011 to describe the pecuniary factors that influence the land-use decision. For simplicity, we consider only whether a farmer participates in the AES (extensive grassland) or not (intensive cropland). Note that this assumption does not display the decision farmers face in reality and should be modified for more applied studies. A farmer chooses the more profitable land use. The profit for cropland depends on various factors like the temporally varying crop selling price p_C [€/t] and the spatially heterogeneous soil quality Q . Thus, the expected net present value varies over time and in space. The annual gross return is given by the function

$$\pi_C(p_C, Q, f) = p_C Y(Q, f) - \omega f - \nu, \quad (4.1)$$

where $Y(Q, f)$ [t/ha] is the crop yield given by the Mitscherlich-Baule yield function (see Appendix). It depends on the beta distributed soil quality $Q \sim \beta(1.15, 2.05)$ and the agricultural intensity f for fertilizer and pesticide use which is assumed to be optimized. Parameter ω [€/ha] describes the input cost and ν [€/ha] fixed costs of cropland. Extensive grassland is assumed not to be affected by soil qualities or temporally varying factors. The annual gross return is thus given by the constant term

$$\pi_G = p_G + s_G + u_s, \quad (4.2)$$

where p_G is the grassland revenue [€/ha]. The subsidies for extensive grassland are denoted by s_G [€/ha]. u_s describes the strength of the preference for one land use as a result of social pressure from neighbours. It is given by the *social utility* function for non-pecuniary effects described below. Note that u_s can be either positive or negative and thus favor either cropland or grassland use, respectively.

The land-use decision consists of an optimization problem to maximize expected profits for a given time horizon H when starting at time t_0 :

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

δ is the discount rate and π_t is the expected gross return in year t according to (4.1) and (4.2). Parameter C_t serves to include the assumption that a change from one to the other land use is accompanied by additional conversion costs. For all details and parameter values of the model, we refer to the Appendix.

4.2.2.2 Descriptive norms

To determine the effect of descriptive norms we assume that farmers are affected by the behaviour of their Moore-neighbours⁴. Let g be the number of Moore-neighbours with grassland use, $g = 0, 1, \dots, 8$. Then, following Henderson et al., 2016a, social utility can be implemented by a sigmoidal function of g :

$$u_s(g) = \frac{m}{1 + e^{-k*(g-g_0)}} - \frac{m}{2a}, \quad (4.3)$$

where $m \geq 0$ controls the maximum value for social pressure. In the following, m will be denoted as the *sociality coefficient*. Parameter k gives the slope at g_0 , the midpoint of the curve. Figure 4.2 shows a graph of u_s (lower, solid blue curve). If $m = 0$ (Figure 4.2, dashed line), we will call our model the *classical economic model*, which coincides with Barraquand and Martinet, 2011. It represents the case without social norms where decisions are exclusively based on profit maximization. If $m > 0$, we will call our model the *socio-economic model*. A farmer is then, in addition to pecuniary factors, influenced by the land use performed in the neighborhood.

Parameter $a > 0$ defines the effect of informational campaigns or nudging for the promotion of the scheme. $a = 1$ represents the baseline case without additional information. Then, farmers have on average no preference for one or the other land use. Informational campaigns that should encourage farmers to participate in the AES are

⁴ Eight cells that surround the selected cell

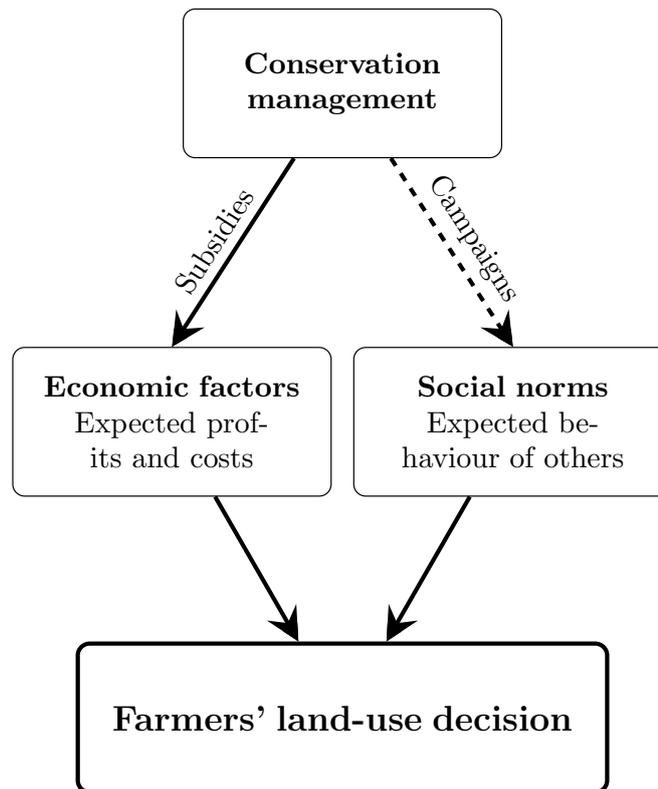


Figure 4.1: Conceptual framework for the land-use decision process of farmers. Campaigns are a potential extension to existing schemes and therefore included with a dashed arrow.

realized by a shift of u_s upwards, $a > 1$ (see Figure 4.2, upper, solid red curve). That is, with nudges, utility for grassland increases compared to cropland. The model with shifted utility function will hereafter be referred to as the *socio-economic model with nudges*.

Note that the utility function is not validated with data or mechanistically driven. However, a sigmoid function is commonly assumed (Lade et al., 2013; Tavoni et al., 2012) and complements game-theoretical research on quantifying non-pecuniary values.

4.2.2.3 Numerical simulations

Numerical model simulations are performed for the classical economic model ($m = 0$), as well as for the socio-economic model in the baseline case ($m > 0$, $a = 1$) and the socio-economic model with nudges ($m > 0$, $a > 1$). For the model comparison with the PROFIL data of the applications for B1 and B2 schemes, an initial grassland share of 0.1% is chosen and randomly distributed over the grid. A grid size of 250×250 is calibrated such that the classical economic model predicts the correct grassland proportion for B1 applications. Due to the simplified situation in the model, it is not possible to scale the grid to an appropriate proportion of agricultural land in Lower Saxony and Bremen.

For the simulations in Section 4.3.2, the landscape size is reduced for computational reasons to a grid of 50×50 patches. The proportion of participants in the AES is given by the share of extensive grassland in the overall land use. Long-term behaviour of

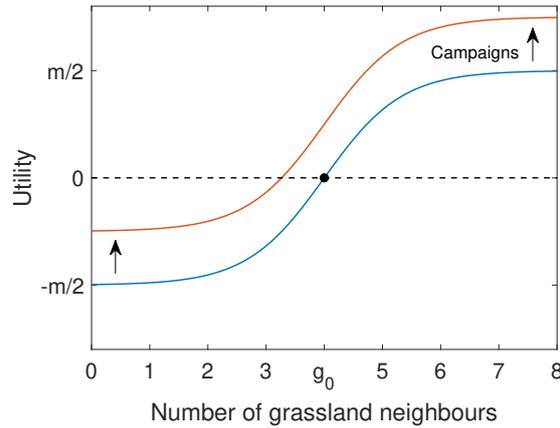


Figure 4.2: Social utility function (4.3) for descriptive norms. Utility is calculated as a function of grasslands in the neighbourhood ($a = 1$, solid blue curve). The introduction of informative campaigns shifts the curve upwards ($a = 2$, solid red curve). Here, $g_0 = 4$ and $k = 1.5$.

the system is analyzed testing initial grassland proportions in steps of 10%. For each initial grassland proportion, 50 stochastic replicates are produced to compute the “mean grassland share at $t = 100$ ” to average out random effects. In each replicate, the initial grassland share is distributed randomly in the landscape.

4.3 RESULTS

4.3.1 *Social norms influence AES participation patterns*

The data sets of AES participation we used to motivate the socio-economic model have two key properties regarding their dynamical patterns: firstly, a gradually increasing participation level after the start of (constant) compensation payments and, secondly, a long-term level of participation that does not necessarily match the participation level that leads to maximal profits. The first property is prominent in the numbers of organic farms in the EU (Figure 4.1). 16 out of 28 member states show a gradual increase in participation numbers (red graphs), whereas only three member states show a sudden increase (black graphs). The dynamics of nine member states show different patterns with no clear increase (grey graphs).

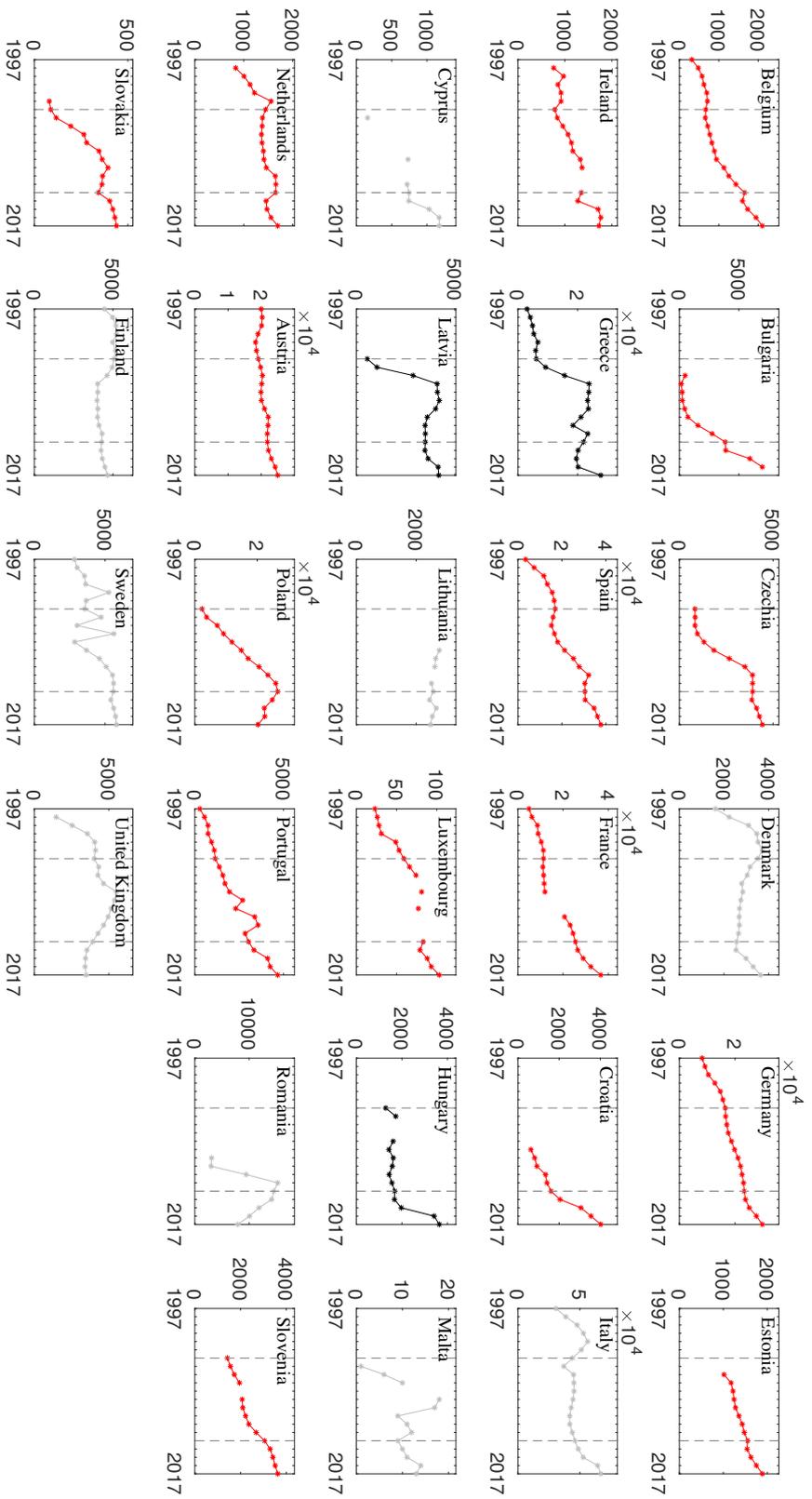


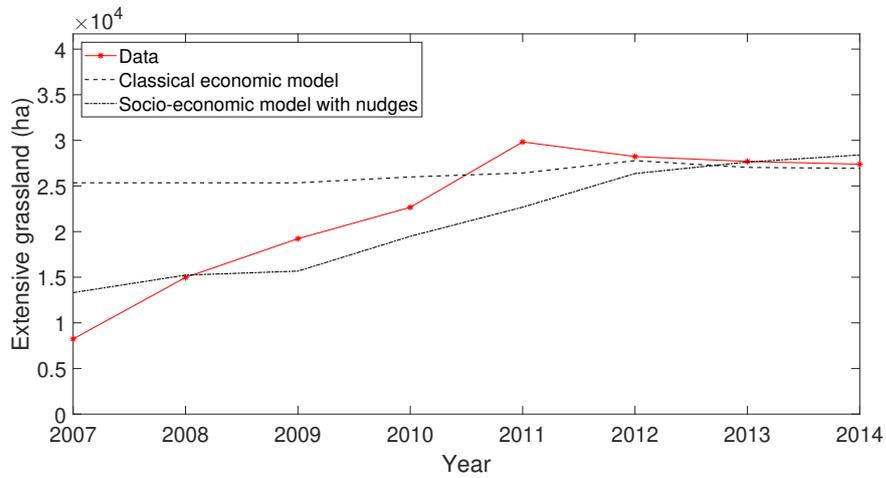
Figure 4.1: Number of organic operators in the EU, divided into member states (indicator OIH_03 in *CMEF Indicator data*). Reforms regarding cross-compliance (2003) and greening-measures (2013) are indicated with dashed lines (Thomas et al., 2019). Data for the member states are colored according to their dynamical pattern: sudden (black) or gradual (red) increases after the start or reform of the scheme or dynamics that do not fall into either of these categories (grey). See Sect. 4.2.1 for classification criteria.

We now show that the socio-economic model presented in Section 4.2.2 can reflect the gradual increase in participation much better than classical economics theory. To that end, we consider the data for the grassland schemes in Lower Saxony and Bremen, Germany. The applications for the B1 and B2 schemes show a gradually increasing trend over time (Figure 4.2, red solid lines), similar to the participation in organic farming in the majority of EU member states, even though the level of subsidization has remained constant over the whole funding period. Figure 4.2 also shows numerical simulations of the classical economic (dashed lines) and the socio-economic model (dashed-dotted lines), under the simplifying assumption that farmers can only decide for or against the schemes. The classical economic model predicts that all farmers for which participating is more profitable do so immediately with the start of the AES. Changes in the participation level after 2007 are only due to variations in the crop selling price. By contrast, the socio-economic model predicts a gradually increasing trend of applications for both B1 and B2 schemes as it is seen in the data. With the start of the AES, only a small proportion of farmers applies to change land use to grassland, which initially inhibits participation of the other farmers. With more and more farmers participating, this increases the social pressure and stipulates continually increasing applications over time. Note that the gradual increase in the data could be also explained by monetary factors, e.g. due to a gradual decrease of the crop selling price. However, since the simulation results are robust to various price scenarios, we conclude that non-pecuniary factors drive the dynamics.

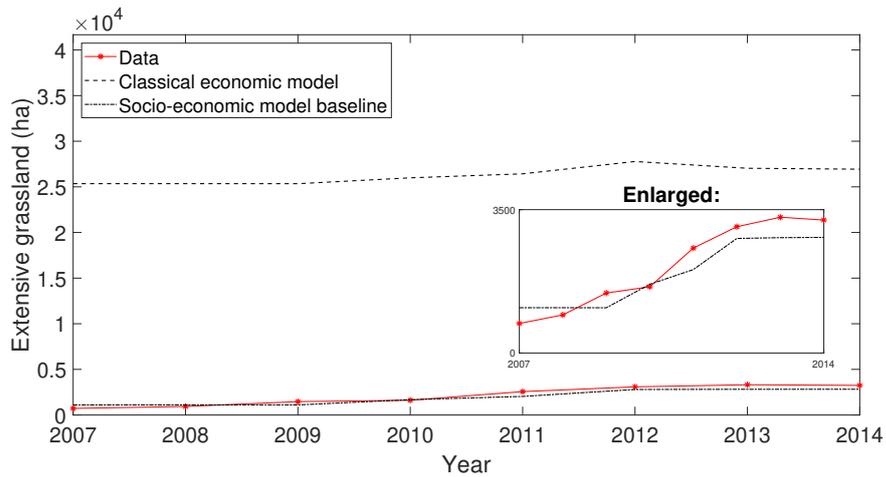
Another property of the PROFIL data in Lower Saxony and Bremen is that many more farmers applied for the action-oriented scheme B1 than for the results-oriented scheme B2 (compare Figure 4.2a and 4.2b) – even though the compensation payments were, with an amount of 110€/ha, the same for both schemes. The classical economic model fails to capture this property. It predicts the same participation level for both the B1 and B2 schemes (Figure 4.2, black dashed lines). If all farmers based their land-use decision only on maximizing profits, we would expect an equal distribution of B1 and B2 schemes due to identical compensation payments. By contrast, the socio-economic model with nudges for B1 ($a = 2$) and without nudges for B2 ($a = 1$) matches the data well (Figure 4.2, black dashed-dotted lines). This choice requires some explanation: the two schemes (B1 and B2) are in fact different. The action-oriented program B1 has a lower risk for the farmer not to receive the payment. Hence, farmers might be more skeptical of B2, consider it less likely to have indicator species on their fields or be less confident in having the expertise in which farming practises help to create good habitats for these species.

This risk perception is not incorporated into the model and will definitely play a big role for the decision-making. Thus, it is not only the framing which is different for the two schemes. What we want to address is, however, that the narrative of the two schemes may not account for all (dis-)advantages. A possible advantage of B2 over B1 is that farmers have less restrictions in the farming practises and can bring in their own expertise. Furthermore, the ecological benefits of B2 are directly visible, which assures the effectiveness of the scheme. Finally, the economic outcome of the farming practise itself is more expectable when not being confined to certain actions and can be optimized with learning. In contrast, the ecological impact of B1 is doubtful and restrictions im-

pede flexible reactions to deal with unforeseen circumstances (e.g. weather). For this reason, we suggest that the B1 and B2 schemes are presented by government agencies or perceived by farmers differently, namely in such a way that justifies the choice of the socio-economic model with nudges for B1 and without nudges for B2.



(a) B1 applications



(b) B2 applications

Figure 4.2: Areas for which farmers applied for B1 and B2 payments in Lower Saxony and Bremen (Germany) compared with predictions by the classical economic (dashed) and the socio-economic model (dashed-dotted). A subsidy level $s_G = 110$ is used according to the data. Parameter values $m = 300$, $k = 1.5$, $g_0 = 4$ are chosen for the socio-economic model. Additional campaigns $a = 2$ in (a). Data from Reiter et al., 2016.

4.3.2 Implications for modelling social norms

We now provide a theoretical model analysis to derive general rules for dynamical participation patterns in the presence of social norms. We are interested in both the tempo-

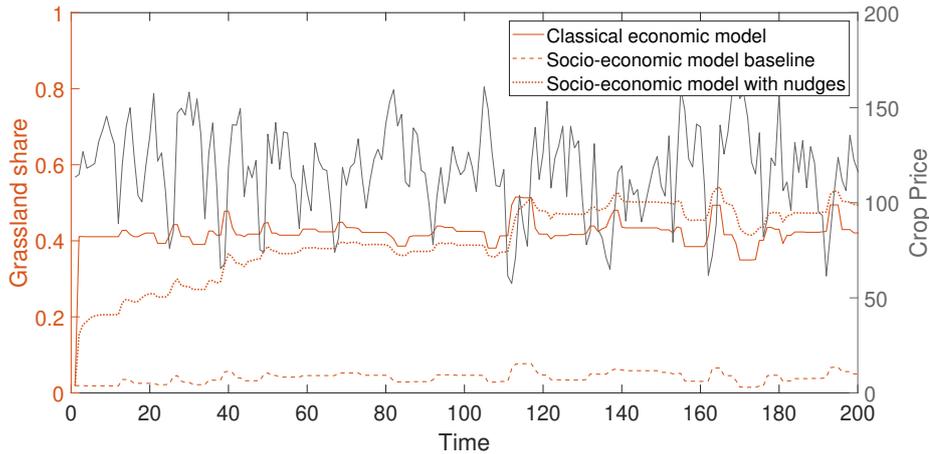


Figure 4.3: Grassland share in the landscape under different model assumptions (red, left y-axis) and crop price over time (grey, right y-axis). Initial grassland share: 1%, economic parameter: $s_G = 110$, parameters for utility function: $m = 300$, $k = 1.5$, $g_0 = 4$, nudging parameter: $a = 1.5$.

ral development of participation immediately after the start of an AES (i.e. the transient dynamics) and the participation level in the long term (i.e. the stationary behaviour).

4.3.2.1 Transient dynamics

The participation level after the start of an AES crucially depends on the model assumptions (Figure 4.3). The classical economic model (red solid line) predicts an instantaneous jump in the grassland share right in the first year of the AES and no further trend over time. Fluctuations are due to crop price variability (grey solid line). The subsidy level of $s_G = 110$ [€/ha] results in an average grassland share of around 40%. The existence of social norms in the model changes the dynamical behaviour.

The socio-economic model in the baseline (dashed line in Figure 4.3) predicts a grassland share that is much lower (at around 5%) and barely increasing. Since the initial grassland share is low, social norms inhibit AES participation. Cropland is dominant in the surrounding of every patch and, thus, farmers do not choose extensive grassland even if it was more profitable. Note that the situation can change if the initial grassland share is larger; this will be discussed in Section 4.3.2.2.

The socio-economic model with nudges (dotted line in Figure 4.3) shows a gradual increase of the grassland share over the first 110 time steps up to 40%. Due to the preference for grassland, less participating farmers in the neighbourhood are required to push farmers to adopt the grassland scheme. After the drop in the crop price at around $t = 110$, the average grassland share increases to a level of around 50% and exceeds the participation level in the classical economic model. Interestingly, the grassland share does not decline when the crop price increases again. Thus, the long-term dynamics in the classical economic model and the socio-economic model with nudging are similar, even when nudging slightly elevates participation levels. Only the transient phase is different.

The average level of participation is a result of an interplay between different factors: the varying crop price and the level of subsidies determine the pecuniary factors which

can vary over time. The initial land-use is spatially heterogeneous and determines the effect of social pressure. Note that the land-use also strongly depends on the heterogeneous soil qualities of the fields, which is not discussed in this paper but addressed in Vortkamp et al. (2020).

4.3.2.2 Long-term participation

In the following, we investigate the impact of social norms on the long-term success of an AES, indicated by the mean grassland share at $t = 100$. Figure 4.4 shows this as a function of the strength of social norms, indicated by the sociality coefficient, and for different initial grassland shares. When social norms play a minor role for the decision (i.e., small sociality coefficient m), a long-term grassland share of around 50% can be identified for all initial conditions. That is, the system has a unique stable equilibrium where all initial conditions lead to. This holds not only for the baseline socio-economic model (Figure 4.4a) as well as for different intensities of campaigns (Figure 4.4b-c). Thus, campaigns only take effect when social norms affect the land-use decision strongly enough.

Now, we consider the impact of stronger social norms and first focus on the baseline case of the socio-economic model ($a = 1$). For increasing sociality coefficients, the mean long-term grassland share steadily decreases, as long as approximately $m < 400$. For even larger sociality coefficients, the long-term behaviour depends on the initial conditions. The majority of initial conditions continue the declining trend and result in a long-term grassland share of 0% for $m > 400$ (dark curves in Figure 4.4a). By contrast, a few initial conditions with large initial grassland shares reverse the declining trend and exhibit an increase for $m > 400$ (light curves in Figure 4.4a). That is, social norms have a non-monotonous effect if the initial grassland share is large. We note two key results for the baseline socio-economic model. First, the tendency of decreasing long-term grassland shares in response to stronger social norms reflects that farmers often refuse to participate in AES even if it was more profitable. Thus, farmers adopt AES less than expected under the assumption of rational decision-making, as it was seen in the B2 application data. Second, for large sociality coefficients the system reveals multistability. That is, the initial participation level is crucial for the success of AES in the future. When a critical proportion of participating farmers is exceeded, the system approaches a different stable state with another long-term grassland share. However, in the baseline case, quite large initial grassland proportions are required to prevent the system from being locked in a zero long-term grassland share for $m > 400$. In the remainder, we additionally consider the impact of campaigns. First, we focus on the socio-economic model with an intermediate level of nudges ($a = 1.5$). Figure 4.4b reveals an increase in the long-term grassland share in response to increasing sociality coefficients, for all initial conditions provided that $m < 200$. This contrasts the declining trend for the baseline socio-economic model in the same parameter range, even though the subsidy level remained the same. For approximately $m > 200$, the long-term outcome again depends on the initial grassland share. The multistability is more pronounced and occurs over a wider parameter range than in the baseline case. There seem to be two dominating branches of curves, one leading to zero grassland use for small initial grassland shares and one leading to complete grassland use for large initial

grassland share. This indicates a fragile system that tips to either very low or very high grassland use. The simulations suggest that, if social norms are present, campaigns can push the system to higher grassland shares, except for high sociality coefficients ($m > 500$) in combination with low initial grassland shares (≤ 0.3). Second, stronger nudging ($a = 2$) effectively eliminates multistability from the system (Figure 4.4c). For a given value of m , all initial conditions approach the same long-term grassland share, except for $550 < m < 600$. The long-term grassland share steadily increases from about 50% to almost 100% in response to an increasing sociality coefficient. That is, for high values of m the preference for grassland is so strong that even if the initial grassland share is almost zero, many farmers are pushed by the norm to participate in the grassland scheme. This may be not realistic in the context of AES and parameters potentially need to be adapted to interpret the result more precisely. However, it can help to understand the positive effects of campaigns if decisions are affected by social norms.

We note three key effects of informational campaigns. First, as they increase the preference for grassland use, they achieve an higher participation levels in the AES. This holds true for all initial grassland shares if social pressure is weak (small values of m) or if the nudging is strong (large value of a). Second, while social norms have the tendency to lock in small initial grassland shares in reinforcing feedback loop, campaigns have the potential to counteract this feedback structure and steer the grassland use into the reversed direction.

4.4 DISCUSSION

Systems like agricultural landscapes are complex. Different parts of the systems can be described by different disciplines. The value of multidisciplinary work is to bring different disciplines together and mediate between actors. In this paper we developed a socio-economic model for farmers' decision-making when AES are available and thereby combine approaches from classical and behavioural economics. The sigmoidal utility function with no preference for one land use complements game-theoretical research on quantifying non-pecuniary values (Le Coent et al., 2018) and can explain why AES participation levels are often lower than expected (Bikhchandani et al., 1992; Burton et al., 2008; Lobley and Potter, 1998; Mathijs, 2003; Nyborg et al., 2006). When a farmer perceives that only few others participate in a scheme, it hinders him or her from participation even if compensation payments were large enough to stipulate participation from a purely economic point of view. This is in line with Le Coent et al., 2018 who report that it is observed in practise that some farmers are extremely reluctant to switch to new farming practices even when a payment level is above additional costs and income foregone.

The socio-economic model with nudges captures the situation when farmers are provided with information that promotes the scheme and can be sufficient to trigger a higher proportion of farmers to participate in the AES. This confirms empirical studies which have demonstrated that how a policy is framed and promoted can significantly alter the perception and reaction of the target group of this policy (Bikhchandani et al., 1992; Kuhfuss et al., 2016; Nyborg et al., 2006; Sutherland and Darnhofer, 2012; Thomas et

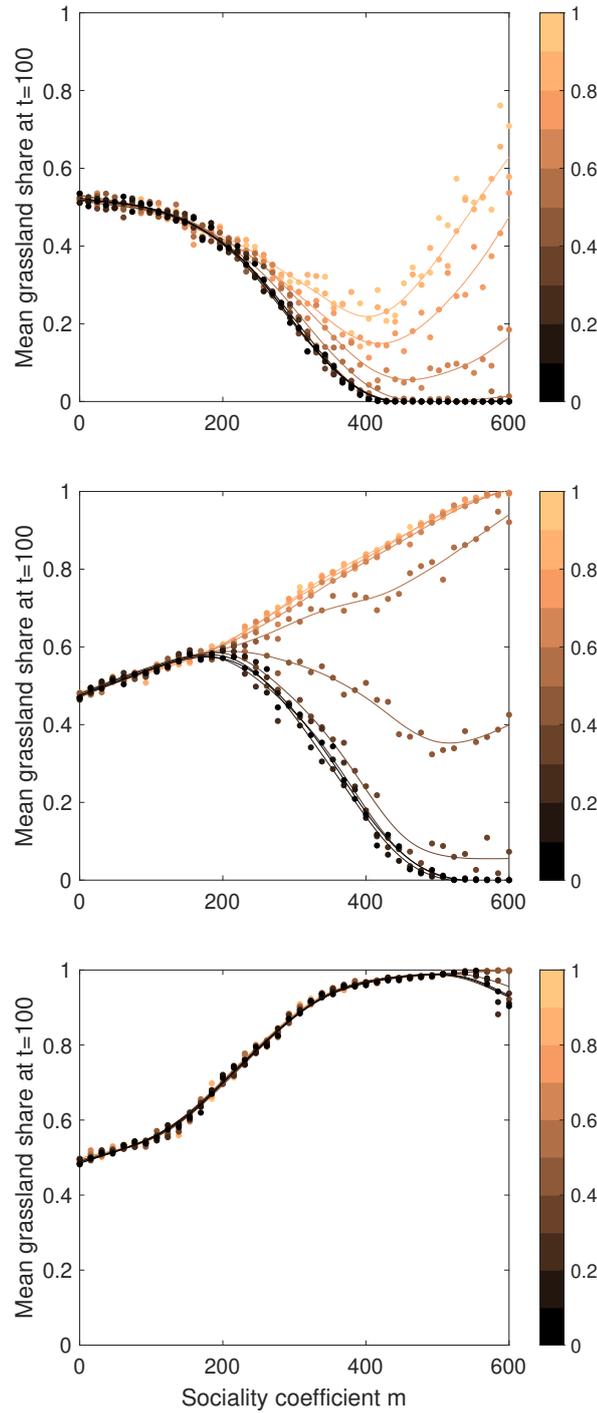


Figure 4.4: Mean long-term grassland share in the landscape as a function of the sociality coefficient $m \in [0, 600]$. Without campaigns: $a = 1$ (a) and with nudges: $a = 1.5$ (b), $a = 2$ (c). Initial grassland share grouped in 0.1-steps indicated by the colour bar. 50 replicates for each initial condition. Lines connect outcomes for the same initial conditions. Other parameter values $k = 1.5$, $g_0 = 4$, $t_{\text{end}} = 100$, $s_G = 120$.

Table 4.1: Examples of steadily increasing AES participation patterns

Study	Type of AES	Location	Funding period
Lobley and Potter, 1998	environmentally sensitive area	England, UK	1987–1996
Johann Heinrich von Thünen-Institut, 2008a	extensive grassland	Bremen, Germany	2000–2006
Johann Heinrich von Thünen-Institut, 2008b	extensive grassland	Lower Saxony, Germany	2000–2006
Ministerio de Agricultura, Ramaderia, Pesca i Alimentació, 2016	forest scheme	Catalonia, Spain	2007–2013
Johann Heinrich von Thünen-Institut, 2016	extensive grassland	North Rhine-Westphalia, Germany	2000–2004
Reiter et al., 2016	extensive grassland	Lower Saxony, Germany	2007–2014
Réseau Rural Français, 2017	forest scheme	France	2007–2013
Bayerische Landesanstalt für Landwirtschaft, 2018	extensive grassland	Bavaria, Germany	2007–2017

al., 2019). A farmer develops a positive attitude to the scheme and participates even if only few farmers in the surrounding do so. We used this to explain why two grassland schemes in Lower Saxony and Bremen (Germany) that compensate farmers equally are adopted differently. We are aware that farmers rather participate in action-oriented schemes (Sutherland and Darnhofer, 2012), which may be considered as less risky to receive payments. However, a biased description that confronts farmers with the risks of a results-based scheme rather than the opportunity to bring in their own expertise and flexibility in the farming practise can increase the gap of participation levels between the two. Nudging in campaigns is highly debated, though (Loewenstein et al., 2015). Arguments against framing range from the possibility of misguidance of social norms (Cialdini, 2003) to manipulation of the target group (Kuhfuss et al., 2016). Furthermore, one should have in mind that the effect of framing is highly context-dependent, which is why it is hard to optimize environmental campaigns (Mosler and Martens, 2008; Thomas et al., 2019).

However, both versions of the socio-economic model (baseline and with nudges) could produce gradually increasing participation patterns. This is not an exceptional property of the German and the European data sets considered in this paper. We have found similar gradual increases in AES participation all over Europe, a collection of which is listed in Table 4.1. Direct responses after the start of an AES as predicted by classical economic theory are only likely if changes in the farming practise are small (McCracken et al., 2015; Schramek and Schnaut, 2004; Sutherland and Darnhofer, 2012).

Finally, our analysis of the long-term behaviour shows that social norms, if strong enough, can push a monostable system to a region of multistability. How is that possible? Villanueva et al., 2015 performed a choice experiment and categorized farmers in: potential participants (in AES), non-participants and farmers willing to participate but having different requirements. In the light of our model simulations we can argue that

the behaviour of the last group finally depends on positive feedbacks by the behaviour of others. Thus, the proportion of the last group may determine how pronounced the branches in Figure 4.4 are. Empirical explanations for multistability are diverse. One explanation is that AES give time to acquire new skills and better knowledge of the risk, leading to long-term behavioural changes (Kuhfuss et al., 2016). Transitions towards conservation-oriented attitudes through scheme participation are also possible (Wilson and Hart, 2001). Moreover, social norms can supercharge non-pecuniary but selfish motivations (warm-glow feeling) and thus increase the likelihood that farmers maintain pro-environmental practices (Kuhfuss et al., 2016). If the decision-making process does have multiple stable states, it shows that not only the decision towards an AES is represented insufficiently by classical economic models but also the long-term effects are not captured well. The so called “end-of-contract problem” is not addressed in this study but a possibility for further research (Kuhfuss et al., 2016).

The question of determinants of economic decisions in an agricultural context remains controversial in the literature (Bikhchandani et al., 1992; Henderson et al., 2016b; Lobley and Potter, 1998; Pavlis et al., 2016; Willock et al., 1999b). We do not wish to quantify the impact of social norms and informational campaigns on the decision making process of farmers. But the limited success of many AES has shown that the assumption that farmers decision is just profit-based is too short-sighted and new concepts are needed (Henderson et al., 2016a; Thomas et al., 2019). This becomes obvious by comparing the participation patterns of the action-based scheme B1 and the results-based scheme B2. The former scheme is much more attractive to farmers but its impact on conservation is doubtful. The latter, on the contrary, is rarely adopted by farmers, even if it contributed more to the goal of biodiversity maintenance. It is crucial to understand the motives leading to or against participation in an AES. To that end, we presented a simple approach and included social norms in a mathematical model for farmers' land-use decision-making. Model simulations suggest that when social norms influence land-use decisions, conservation will probably not be successful just by allocating money to compensate farmers for foregone profits.

A deeper understanding of how to integrate non-pecuniary factors in socio-economic models is still pending. A suitable parameterisation of the utility function is desirable and it needs to be investigated how a change in attitudes can be reflected in the model (nudging, campaigns). However, the advantage of the presented work is that we can deliver a dynamical model that confirms findings from behavioural economics and matches participation patterns in the literature.

Based on the results, we formulate implications for the future design of AES that need to be treated carefully due to the high level of uncertainty. Conservation agencies or policy makers that design AES often use only the tool of subsidies or taxes as monetary incentives. However, if decisions are affected by social norms, informational campaigns or nudging that promote a scheme can be a powerful tool as well. The advantage of nudging is that it often comes at low costs, is widely applicable and can help to improve acceptance. If campaigns fail, we have seen that this can be due to a minor role of social norms for the decision-making. Furthermore, one should have in mind that campaigns can only support, not replace, subsidy instruments. AES should be designed such that farmers are involved with their knowledge and skills to use the so-

cial norm for conservation (Thomas et al., 2019; Wilson and Hart, 2001; Wynne-Jones, 2013). Farmers that are fundamentally against AES (e.g. because they think it is contrary to good agricultural practice or don't like people telling them what to do and not to do (Lobley and Potter, 1998)) will also not change their attitude with informational campaigns or different framing (Sutherland and Darnhofer, 2012). These should not be the targeted group of a scheme or could rather be targeted with a results-based scheme. If social norms are present, land-use decisions are influenced by the self-concept and social identity and how a scheme is perceived (Goldstein et al., 2008) which can be addressed by campaigns and an integration of AES in the farming practise (Wilson and Hart, 2001; Wynne-Jones, 2013).

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APPENDIX

4.A ECONOMIC ASSUMPTIONS

4.A.1 Price variability

The crop selling price at time t is given by

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

where B is a coefficient of autocorrelation, $p_{C,t-1}$ is the crop selling price in the previous time step and $\epsilon_t \sim N(0, 20)$ is a normally distributed random variable. 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).

4.A.2 Price expectations

Farmers' expectation at time $t - 1$ of crop selling price in $n + 1$ time units are given by:

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

Agricultural yield

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

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

4.A.3 Optimal input use

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

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

4.A.4 Parameter values

We choose the economic parameters following Barraquand and Martinet, 2011. They are listed in Table 4.A.1.

Table 4.A.1: 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	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]

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.

5.1 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 inbreeding depression (Allen et al., 2005; Gascoigne and Lipcius, 2004; Gascoigne et al., 2009; 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 some-

how paradoxical since a higher extinction risk is of particular relevance to understanding threats to populations at low densities which are 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 5.1. 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, 2005). 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). 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 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 5.2, 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 5.3, we discuss trade-offs between conservation success and agricultural production in the presence of an Allee effect. We estimate conserva-

Table 5.1: 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

tion costs in different scenarios. Finally, we analyze the relevance of the spatial habitat configuration. In Section 5.4, we conclude and discuss the results.

5.2 MATERIAL AND METHODS

5.2.1 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 5.1). 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 metapopulation¹ 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

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, are used.

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 Figure 5.1.

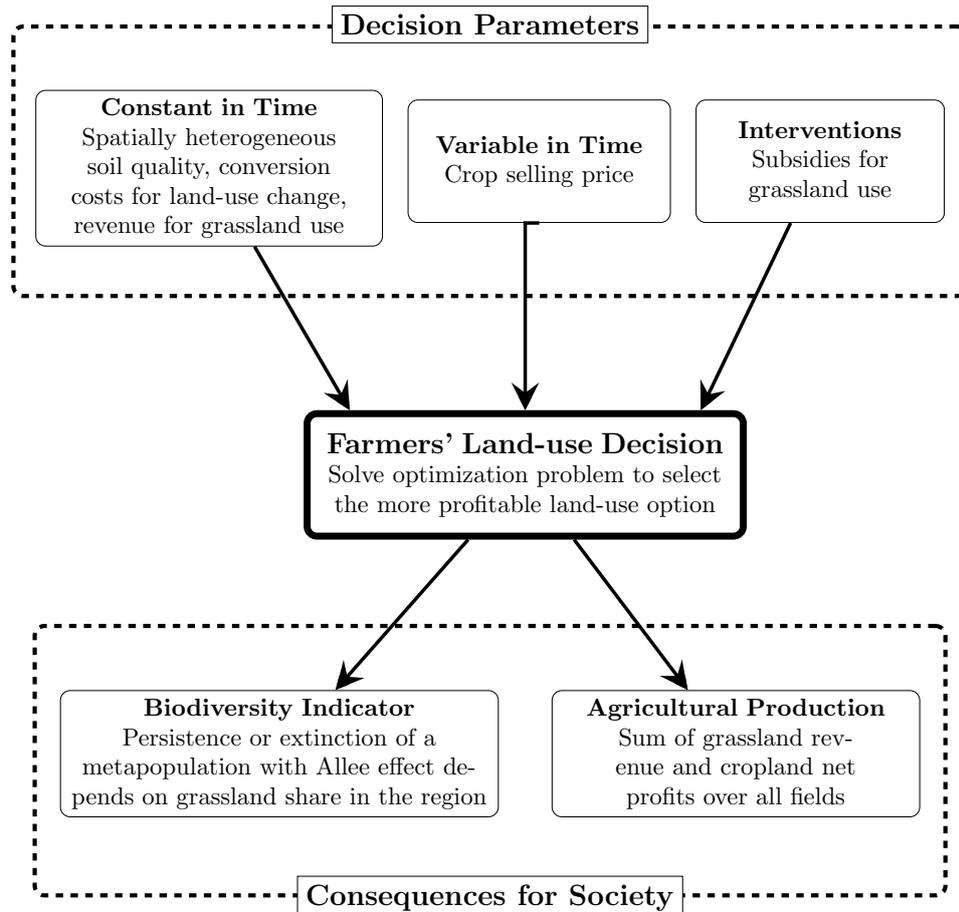


Figure 5.1: Conceptual framework for the process of land-use decision. An optimization problem is solved to maximize the farmers' profit. The two outcome dimensions are affected by the decision.

5.2.1.1 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 Figure 5.2 (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 .

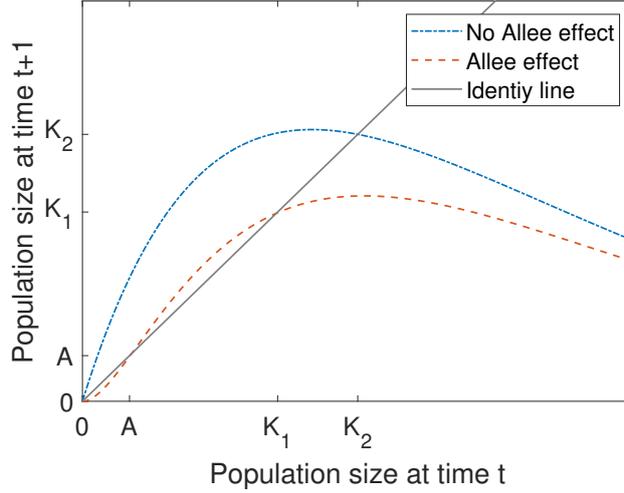


Figure 5.2: Population size at time $t + 1$ as a function of population size at time t . Reproduction modeled by a deterministic version of Equation (5.1) without Allee effect ($\Phi = 0$; blue dash-dotted curve) and with Allee effect ($\Phi > 0$; orange dashed curve). The gray solid (identity) line denotes the case where the population size at time $t + 1$ equals the population size at time t .

as in models without Allee effect (Figure 5.2, 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.

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

$$\mathbb{E}(N_{i,t_+}) = N_{i,t} \underbrace{e^{r_G \left(1 - \frac{N_{i,t}}{K}\right)}}_{F(N)} \underbrace{\frac{N_{i,t}}{\Phi + N_{i,t}}}_{G(N)}, \quad (5.1)$$

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:

$$\mathbb{E}(N_{i,t_+}) = N_{i,t}e^{r_C}. \quad (5.2)$$

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 5.A.1). Parameter values of the ecological model are provided in 5.A.3.

5.2.1.3 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

$$\pi_G = p_G + s_G, \quad (5.3)$$

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

$$\pi_C(p_C, Q, f) = p_C Y(Q, f) - \omega f - \nu_c, \quad (5.4)$$

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 5.A.2 and 5.A.3, 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 Equations (5.3) and (5.4). Parameter C_t serves to include the assumption that a change from one land use to the other is accompanied by additional conversion costs.

5.2.2 Quantities of interest

5.2.2.1 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 production² 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 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.

5.2.2.2 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 5.3). 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 5.3.

5.2.3 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 5.4a. 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>).

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

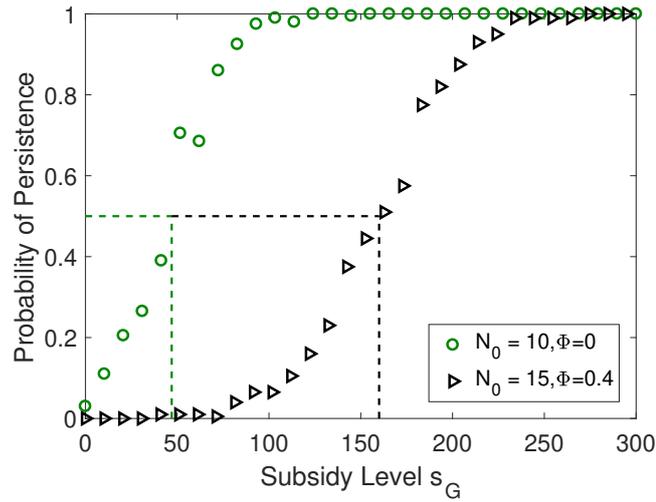


Figure 5.3: Persistence probability as a function of the subsidy level s_G . Green circles: Initial local population size $N_0 = 10$ and no Allee effect $\Phi = 0$; black triangles: $N_0 = 15$ and $\Phi = 0.4$. Dashed lines indicate the subsidy level required for 50% persistence probability.

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 Figure 5.4b.

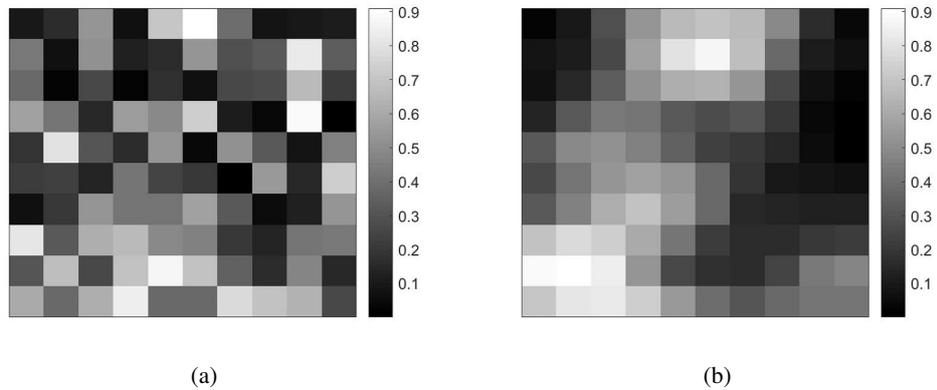


Figure 5.4: Beta distributed soil quality Q in the landscape, spatially uncorrelated in (a) and arranged in a random field to obtain spatial clumping in (b). Q is normalized in the range $[0, 1]$, which means that it represents an index of the potential yield of the agricultural field (i.e., the maximal 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.

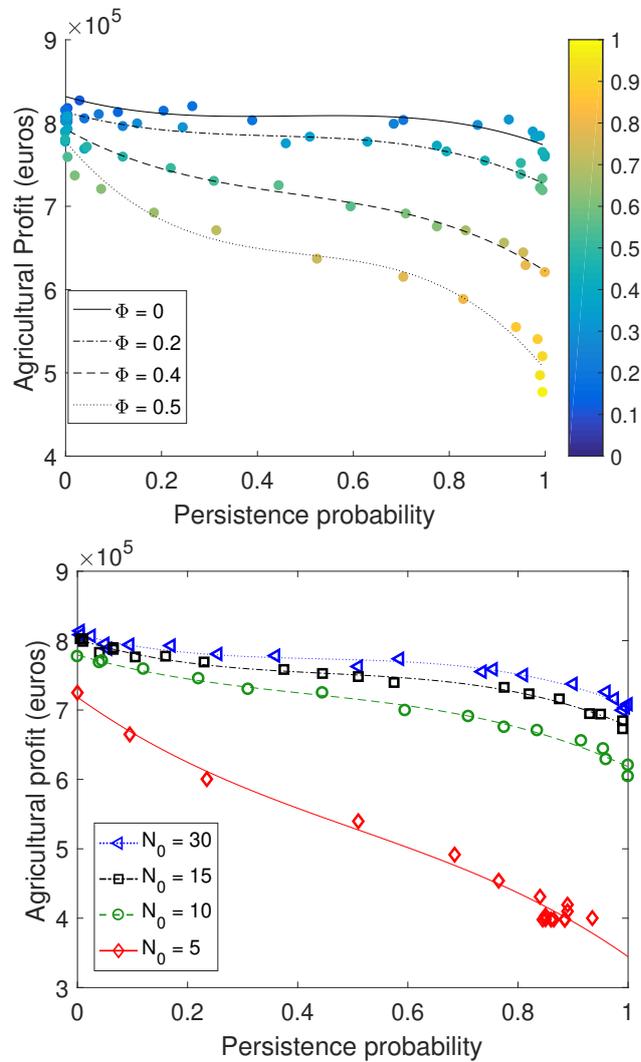


Figure 5.1: Production Possibility Frontier of the dynamic landscape for different values of the Allee parameter Φ (a) and different initial population sizes N_0 (b). The color bar in (a) indicates the mean grassland proportion in the landscape. Curves are polynomials of order 3 fitted by least squares method, ignoring values for persistence probability equal to 0 or 1. Monte-Carlo simulations with 200 runs. In (a), $N_0 = 10$. In (b), $\Phi = 0.4$.

5.3 RESULTS

5.3.1 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 5.1a, solid line, or Barraquand and Martinet, 2011). That is, the opportunity costs for improving the ecological outcome in the landscape are low. Figure 5.1a 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 Figure 5.1 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.

5.3.2 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 Figure 5.1b. 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 small numbers) are less effective.

Figure 5.B.1 in Appendix 5.B 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 5.1b. Thus, the big trade-off for $N_0 = 5$ must be due to the Allee effect.

5.3.3 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 5.2 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 5.2. 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 Figure 5.2 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 Figure 5.2, fitted curves). If we consider the case of $N_0 = 5$, for instance, 50% persistence probability can be achieved with a subsidy level of $s_G \approx 100$ [€/ha] when the Allee parameter is small ($\Phi = 0.1$). By contrast, s_G needs to be at a level of almost 250 [€/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.

5.3.4 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 5.3a shows time series of global population size for the cases with and

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

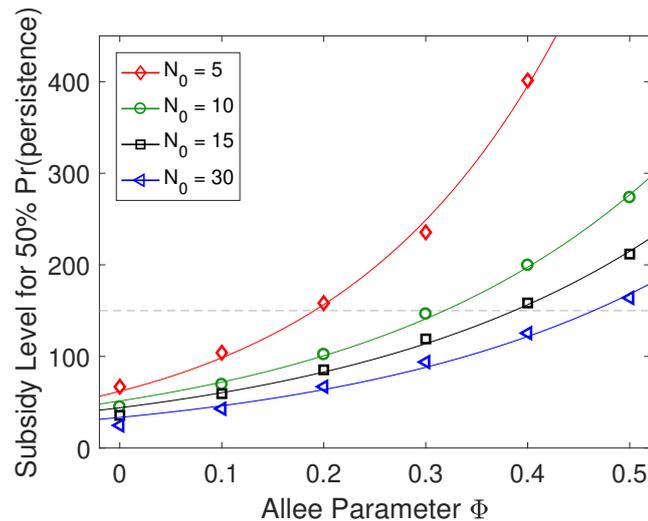


Figure 5.2: Subsidy level that is required to achieve 50% persistence probability. Note that for $N_0 = 5$ and $\Phi = 0.5$ the conservation target cannot be achieved by any subsidy level; no data point exists. Dashed grey line indicates the mean subsidy level for extensive grassland in Germany in 2015 (Bundesministerium für Ernährung und Landwirtschaft, 2015).

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 Figure 5.3b): 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 Figure 5.3a. 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.

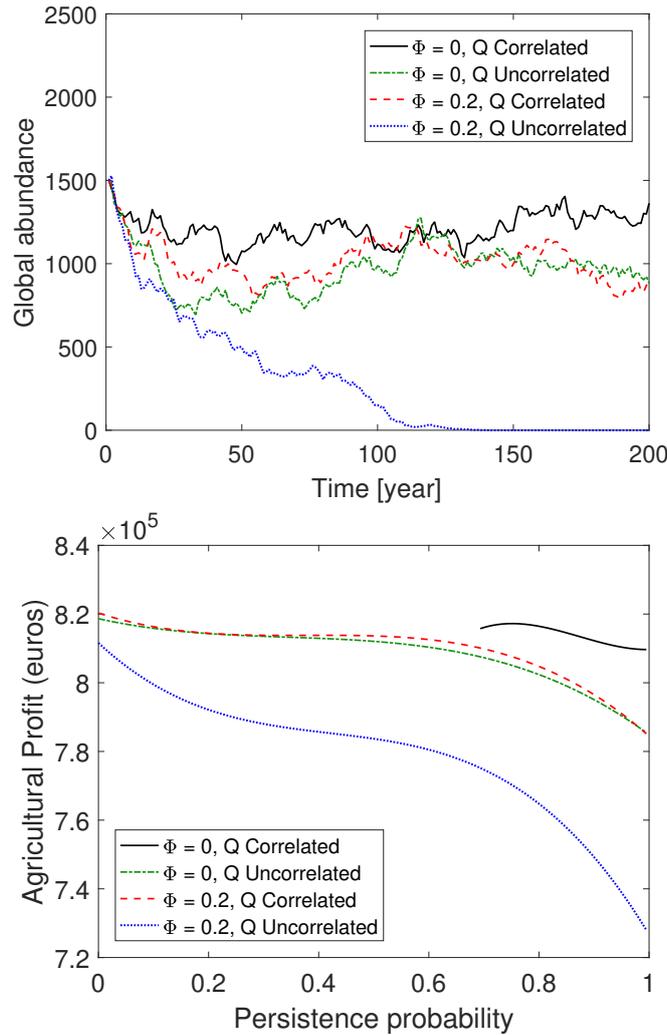


Figure 5.3: Time series (a) and Production Possibility Frontier (b) of the dynamic landscape for $\Phi = 0$ and spatially correlated soil quality Q (black solid line), $\Phi = 0$ and spatially uncorrelated soil quality Q (green dot-dashed line), $\Phi = 0.2$ and spatially correlated soil quality Q (red 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.

5.4 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 5.1). 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 the 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 costs⁴ 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., 2011b). Some studies state that land sparing is a more promising strategy for minimizing negative impacts of food production (Phalan et al., 2011b) 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, 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

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

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.

ACKNOWLEDGEMENTS

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APPENDIX

5.A MODEL ASSUMPTIONS

5.A.1 *Ecological Assumptions*

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.

5.A.2 *Economic Assumptions*

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).

Price expectations

Farmers are assumed to make rational price expectations given by

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

Agricultural yield

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

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

Optimal input use f^*

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

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

5.A.3 Parameter values

The economic parameters are chosen following Barraquand and Martinet, 2011. They are listed in Table 5.A.1.

Table 5.A.1: 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]

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 5.A.2.

Table 5.A.2: 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]

5.B PRODUCTION POSSIBILITY FRONTIER WITHOUT ALLEE EFFECT

The PPF in Figure 5.B.1 without Allee effect ($\Phi = 0$) for several initial emphasizes that the results in Figure 5.1b are not due to demographic stochasticity but due to the Allee effect.

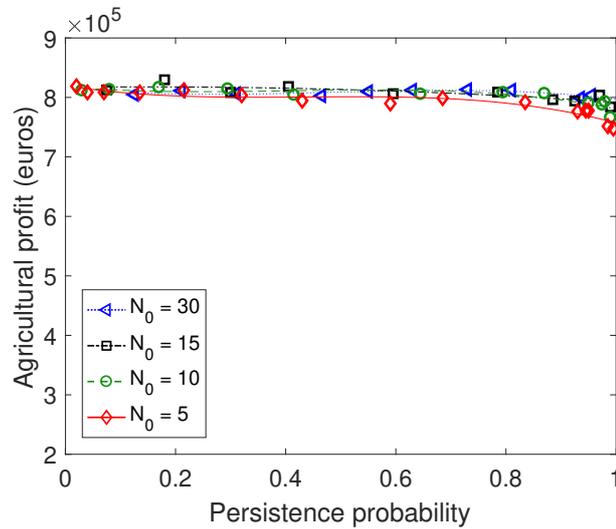


Figure 5.B.1: Production Possibility Frontier of the dynamic landscape without Allee effect ($\Phi = 0$) for different initial population sizes N_0 . Curves are polynomials of order 3 fitted by least squares method, ignoring values for persistence probability equal to 0 or 1. Monte-Carlo simulations with 200 runs.

CONCLUSION

6.1 SUMMARY

An increasing number of interdisciplinary programs integrate ecological and social sciences to study *coupled human-environment systems* (Aspinall and Staiano, 2017; Bauch et al., 2016; Liu et al., 2007). Coupled human-environment systems are often characterized by nonlinear interactions, even in isolation from one another. By coupling, emergent properties and a richer variety of dynamical regimes can arise (Bauch et al., 2016). With the help of quantitative models, complex interactions can be identified systematically towards a holistic understanding of causalities within a system (Aspinall and Staiano, 2017; GLP, 2005). Figure 6.1 shows a conceptual model of a land system by Schaldach and Priess (2008) as an example of a coupled human-environment system. The land system is associated with land use in the human subsystem, e.g. for economic purposes (Aspinall and Staiano, 2017). From the ecological perspective, a land system is seen as land cover which is determined e.g. by hydrological and topographical properties and in turn creates conditions for biological communities. The two subsystems feed back on each other via decision making for land use and ecosystem services provided by nature, respectively. Therefore, it is a nice example for a coupled human-environment system and can be partly identified with the coupled human-environment system of agricultural landscapes investigated in this dissertation. Part I, consisting of **Chapters 2 and 3**, studies the ecological subsystem in more detail to promote a mechanistic understanding of relevant ecological processes in response to changing land use. **Chapter 4**, on the other hand, investigates the interplay of societal and economic factors in the human sub-system. Finally, **Chapter 5** presents a coupled human-environment system to account for the complexity of both sub-systems. The impact of management in the human subsystem on the ecological system is analyzed (Sun, 2019).

For the metapopulation models in Part I, human impact is reduced to single parameters that determine the growth and dispersal parameters for the species in the respective environments. General mechanisms of the effect of dispersal on population viability and size are analyzed. The generic model formulations do not depend on a specific organism and therefore can have numerous possible ecological applications.

In **Chapter 2**, a system of ODEs is used to study a metapopulation in two heterogeneous habitats. The effect of dispersal on the total population density is explored and compared with empirical data which we generated in laboratory experiments on *Escherichia coli*. The studied model system shows a smaller total population density in the presence of dispersal between the patches than in isolated patches. This result is supported by both model and data. A negative r-K relationship, which can be interpreted as stronger density dependence in the habitat with lower resource amount, is identified

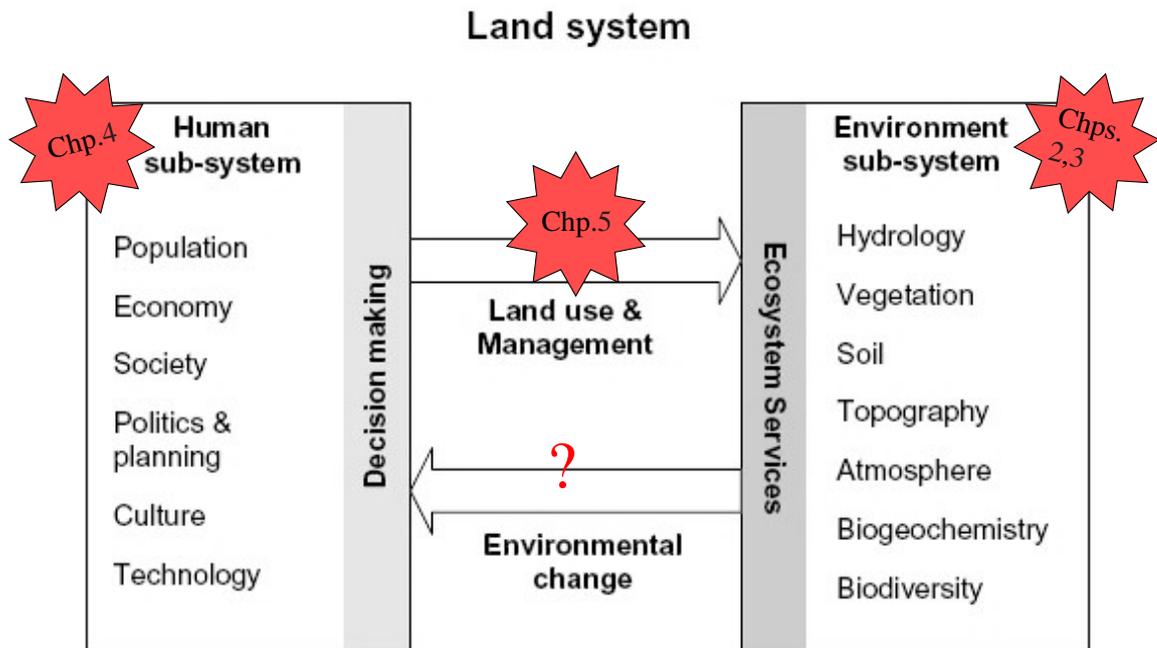


Figure 6.1: Conceptual model of a land system, based on Schaldach and Priess (2008)

as a mechanism leading to reduced population densities with dispersal. Reviewing the literature and determining growth parameters of published population experiments, we find that both positive and negative r-K relationships are possible. This mechanism can be added to the long list of implications of habitat fragmentation and habitat isolation in particular (e.g. Didham et al., 1996; Driscoll et al., 2013; Fahrig, 2017; Fischer and Lindenmayer, 2007; Haddad et al., 2015; Soulé et al., 2004; Villard and Metzger, 2014; Weddell, 2002). Due to the disagreement about fragmentation effects, there is a need for separate investigations of the single effects of habitat isolation, edge and amount (Andren, 1994; Didham et al., 1996; Hobbs and Yates, 2003; Miller-Rushing et al., 2019). On the basis of our results, we question conservation measures such as dispersal corridors or stepping stones that counteract fragmentation but neither habitat loss nor edge effects.

In **Chapter 3**, a discrete-time model of a spatially structured population is presented. The interaction of dispersal, a strong Allee effect and overcompensation is explored. Complex dynamics and multiple attractors are a result of bistability due to the Allee effect and potentially chaotic dynamics in coupled maps with overcompensation (Amarasekare, 1998; Hastings, 1993). Parameter ranges that can protect the spatially structured population from essential extinction are identified (DIPEE). In the case of weak coupling, a state in which one subpopulation density is above and the other one below the Allee threshold can prevent essential extinction. Strong coupling, on the other hand, enables both subpopulations to persist above the Allee threshold when dynamics are (approximately) out of phase. The attractors have fractal basin boundaries. Essential extinction shows well that not only small populations are prone to extinction but immediate collapses also of large populations can occur. The effect of dispersal can be either positive or negative. On the one hand, dispersal can mediate local population

persistence (rescue effect) or reduce overshoots and thus prevent essential extinction (DIPEE). On the other hand, dispersal can reduce local population sizes below the Allee threshold or induce an overshoot and thus cause (essential) extinction. These negative effects are not investigated in this dissertation but should not be neglected. Moreover, the spatial system structure can lead to long transients of persistence that last hundreds of generations before the seemingly safe population abruptly goes extinct. Thus, the comprehensive analysis is fundamental to understand the complex behaviour of the presented system.

Taking the results of these two chapters together, we learn an important lesson for conservation: when the cause of extinction is unknown, it can be fatal to apply a measure that may cause unintended side effects or may not be appropriate (Fryxell et al., 2014): a negative r-K relationship between two habitats of heterogeneous habitat quality leads to negative effects of dispersal whereas movement between homogeneous habitats can promote rescue effects and DIPEE if the population exhibits Allee effects. A ubiquitous recommendation is therefore not possible.

In **Chapter 4**, the ecological component was ignored to study the human subsystem in more detail. Many empirical, qualitative studies have shown that non-pecuniary factors affect farmers' land-use decisions, but the integration in quantitative studies is still sparse (GLP, 2005). The socio-economic model presented in this dissertation integrates descriptive norms in the decision-making process if land can be set under agri-environment schemes (AES). Numerical simulations suggest that social norms can inhibit the participation in AES which runs counter to the *homo oeconomicus* concept. Social norms can therefore serve as an explanation for different participation levels in equally compensated schemes. Action-based schemes are more attractive to farmers but the ecological impact is doubtful. Results-based schemes, on the contrary, are rarely adopted by farmers, even if the contribution to biodiversity maintenance is more secure. Qualitative studies further suggest that direct responses by farmers after the start of an AES are only likely if changes in the farming practise are small (McCracken et al., 2015; Schramek and Schnaut, 2004; Sutherland and Darnhofer, 2012). Gradually increasing participation levels are common and found in many data sets all over Europe. The socio-economic model implemented in this dissertation can capture this transient behaviour. Incorporating non-pecuniary values (social norms) in an economic model can therefore help to close the gap between assumed and observed human behaviour. Conservation will probably fail just by allocating money to compensate farmers for foregone profits without accounting for tradition and norms. Informational campaigns that alter the perception and reaction of farmers are included in the model and can trigger a higher proportion of farmers to participate in the AES (Hynes and Garvey, 2009). Campaigns can only support, not replace, the subsidy instrument, though. Socioeconomic systems, as implemented in this dissertation, can have alternative stable states (Nyborg et al., 2016). It is not clear whether these stable states exist in real agricultural land use systems. If this was the case, not only the decision towards an AES is represented insufficiently by classical economic models but also the long-term effects are not captured well (Kuhfuss et al., 2016). The approach for the socio-economic model used in this dissertation is valid not only in the context of agriculture. It will provide a better understanding how to model human behaviour in economic contexts in a more realistic

manner.

A synthesis and coupling of a human-environment system is presented in **Chapter 5**. The coupled economic-ecological model deals with the challenge to balance biological conservation and agricultural production on private land. The potential for land-use conflicts is high, and failing to account for the complexity (Allee effects) in the ecological subsystem can underestimate the potential for extinctions. Our results suggest marked trade-offs between conservation success and productivity in the landscape. More suitable habitat is required to prevent extinction of the species of interest which implies that conservation is more costly (exponential relationship). Moreover, management is well advised to start as early as possible. This also holds in the absence of Allee effects, but bistability due to the Allee effect makes it hard for population size to recover once it has declined to some critical value. From the political point of view, it will be difficult to justify conservation of a species that is not yet threatened. However, the advantage of the presented quantitative model is that cost-effectiveness of different strategies can be visualized in a Production Possibility Frontier (De Lara and Doyen, 2008). Finally, the effect of spatial arrangement of habitat on population viability is emphasized. Natural or man-made aggregation of suitable habitat can enhance rescue effects from movement between patches and help to prevent extinction. Thus, when payments take a spatial component into account (e.g. agglomeration bonuses (Drechsler et al., 2010; Parkhurst et al., 2002)), the cost-effectiveness of a measure may be increased.

Table 6.1 gives a short summary of the results of this dissertation. However, some limitations and perspectives that are not mentioned in the chapters, are discussed in the following.

6.2 DISCUSSION

6.2.1 *'Simple means general means good'?*

One critical question is how useful simple models as those presented in **Chapters 2** and **3** are to improve management in practice (Lester, 2019). The idea of simplified (strategic) models is to idealize the situation in order to determine fundamental processes that explain ecological phenomena. The principle 'simple means general means good' is criticized by Evans et al. (2013) though, who argue that a simple model may not inform about any real biological system since processes in real systems are interwoven, some reinforcing others, some balancing others (Fryxell et al., 2014). Therefore, a single process identified in a simple model may be overlaid by other effects in real systems (e.g. trophic cascades: Fischer and Lindenmayer, 2007; Fryxell et al., 2014; Shaffer, 1981). This critique is of particular relevance when considering DIPEE as a mechanism to prevent essential extinction (**Chapter 3**). Moreover, deterministic chaos as an explanation for complex population dynamical patterns is often controversial. Different explanations for complex population dynamics invoke stochastic processes interacting with deterministic dynamics (Evans et al., 2013).

However, DIPEE is not specific for the system in **Chapter 3** but can occur also in different systems. Let me introduce an example: consider a tritrophic food chain (resource,

Table 6.1: Summary of the results of this thesis.

Chapter	Model system	Main results	Possible implications for conservation
Chapter 2	<ul style="list-style-type: none"> • ODE system • Logistic growth • Heterogeneous habitats • Empirical data from experiments with <i>Escherichia coli</i> 	<ul style="list-style-type: none"> • Dispersal can be detrimental for the total population density • First experimental demonstration of negative r-K relationship • Review of literature data and calculation of growth parameters indicates positive and negative r-K relationships in real ecological systems 	<ul style="list-style-type: none"> • r-K relationship is a mechanism that can affect consequences of fragmentation • Effectiveness of dispersal corridors and stepping stones that counteract fragmentation but not habitat loss nor edge effects is doubtful
Chapter 3	<ul style="list-style-type: none"> • Two coupled Ricker maps • Allee effect • Possible overcompensation 	<ul style="list-style-type: none"> • Multiple coexisting attractors • DIPEE: new kind of rescue effect • Fractal basins of attraction • Long transients 	<ul style="list-style-type: none"> • Long periods of unnoticed danger with sudden extinction possible • Not only small populations at risk • Connectivity can promote rescue effects
Chapter 4	<ul style="list-style-type: none"> • Coupled socio-economic model • Agricultural landscape • Descriptive norms affecting land-use decisions 	<ul style="list-style-type: none"> • Utility function for social norms • Explains gradually increasing transient dynamics • Multistability in long-term participation • Campaigns can promote participation 	<ul style="list-style-type: none"> • If social norms influence land-use decisions, compensation is not necessarily successful • Framing can alter decision structure
Chapter 5	<ul style="list-style-type: none"> • Coupled economic-ecological model • Agricultural landscape • Metapopulation exhibiting Allee effects 	<ul style="list-style-type: none"> • Marked trade-offs between conservation success and productivity • More suitable habitat is required to prevent extinction if the population exhibits Allee effects • Aggregation of suitable habitat can enhance rescue effects 	<ul style="list-style-type: none"> • Conservation is more costly if a population exhibits Allee effects • Allee effects make land-sparing solutions more attractive • Early interventions are important in the presence of Allee effects

consumer, predator) with logistically growing resource and Holling type II functional responses for predation:

$$\begin{aligned}\frac{dR}{dt} &= R \left(1 - \frac{R}{K}\right) - \frac{x_C y_C C R}{R + R_0}, \\ \frac{dC}{dt} &= x_C C \left(-1 + \frac{y_C R}{R + R_0}\right) - \frac{x_P y_P C P}{C + C_0}, \\ \frac{dP}{dt} &= x_P P \left(-1 + \frac{y_P C}{C + C_0}\right),\end{aligned}$$

where R is the resource density, C the consumer density and P the predator density (McCann and Yodzis, 1994). The resource carrying capacity K as well as x_C , y_C , x_P , y_P , R_0 and C_0 are positive constants. This system can have two co-occurring attractors. Firstly, coexistence of resource and consumer, and extinction of the predator. Secondly, a coexistence attractor between all three species with potentially chaotic predator dynamics (McCann and Yodzis, 1994). If enrichment is sufficiently strong ($K = 1$), the latter attractor disappears and the predator goes extinct for almost all initial conditions. This situation is analogous to essential extinction, because the non-equilibrium attractor disappears in a global bifurcation, causing the predator to go extinct. However, dispersal of the predator between two similar habitats

$$\begin{aligned}\frac{dP_1}{dt} &= x_P P_1 \left(-1 + \frac{y_P C_1}{C_1 + C_0}\right) - \beta(P_1 - P_2), \\ \frac{dP_2}{dt} &= x_P P_2 \left(-1 + \frac{y_P C_2}{C_2 + C_0}\right) - \beta(P_2 - P_1),\end{aligned}$$

with all other equations and constants being equal, can prevent extinction of both sub-

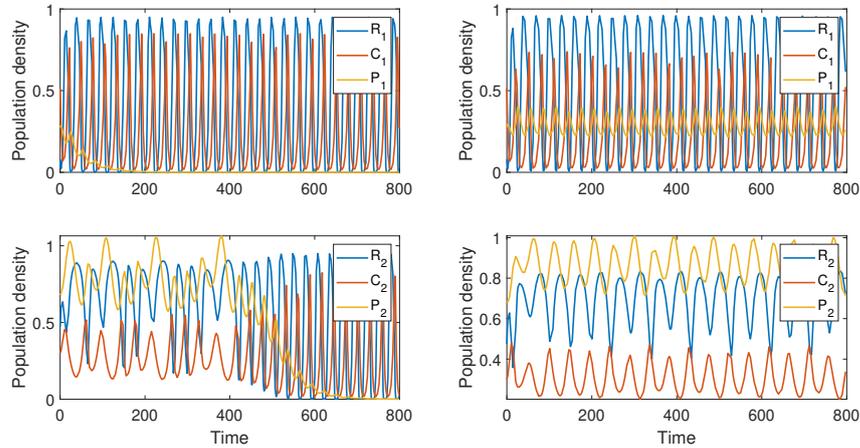


Figure 6.1: Dispersal (right panels, $\beta = 0.01$) can prevent predator extinction in both patches, whereas it is inevitable without dispersal (left panels, $\beta = 0$). Parameter values $K = 1$, $x_c = 0.4$, $y_c = 2.009$, $x_p = 0.08$, $y_p = 2.876$, $R_0 = 0.16129$, $C_0 = 0.5$ based on McCann and Yodzis (1994). Initial condition in both simulations: $(R_{1,0}, C_{1,0}, P_{1,0}, R_{2,0}, C_{2,0}, P_{2,0}) = (0.0778, 0.5147, 0.2758, 0.4746, 0.3010, 0.6792)$.

populations of the predator (Figure 6.1). Thus, DIPEE can occur in other systems with similar dynamical properties, namely one extinction and one persistence attractor, the

latter with potential overcompensation. Moreover, the mechanism is not restricted to two-patch systems. Recall the reproduction function in **Chapter 3**. Numerical simulations for a three-patch system or a grid of habitat patches reveal that dispersal can prevent essential extinction on broader spatial scales as well (not shown here). These examples are neither proof for the existence nor for the visibility of DIPEE in real biological systems. However, the mechanism is robust with respect to the choice of model system and number of patches. Hence, to interpret the results correctly, one should be clear about what 'general' means and which advantages strategic models have compared to tactic models. Simple model formulations make few assumptions and can identify the relevant processes which are at place and then guide the analysis of more extended models by reducing the complexity of a system (De Lara and Doyen, 2008; Evans et al., 2013; Jopp et al., 2010). This procedure is helpful to disentangle the contrasting statements about positive or negative effects of fragmentation on biodiversity (**Chapter 2**). Different combinations of similarly operating processes can lead to seemingly paradox observations in complex systems (Fridley et al., 2007). A further advantage of simple models over tactic models are the multiple application areas. Tactic models, which are more often used for management, are site- and species-specific. In contrast, the models presented in Part I of this thesis, are investigated under the umbrella of conservation but could also be seen in the light of invasive species. Then, extinction is not to be prevented but the desired state (Liebhold et al., 2016).

6.2.2 *Do coupled models improve conservation management?*

It is widely recognized that a deep understanding of how ecosystems function and how human activities interact with them is required in order to guide effective environmental protection (Schmolke et al., 2010). Integrated modelling approaches that incorporate socio-economic as well as ecological aspects therefore become increasingly important (Delacámara et al., 2020; Fulford et al., 2020; Sutherland and Freckleton, 2012). Schmolke et al. (2010) suggest that such models are best to be developed together with practitioners to meet their requirements and address the issues faced by managers and policy makers. Otherwise, the predictive power and value for conservation may remain obscure. The utility function in **Chapter 4** is not validated with data nor is the effect of social norms on land use decisions entirely clear (Allaire et al., 2009). Since many different modes of individual behaviour can lead to the same collective behaviour (Weidlich, 2006), the data might be also explained by a different mechanism than social norms, just with a similar emergent pattern.

However, models can make a range of contributions to the scientific progress and for conservation, not all of them at the interface to management and policy (Epstein, 2008; Lester, 2019). Different modelling purposes can be, inter alia, the exploration and description of ideas and theories, demonstration of concepts or the understanding of general principles and patterns (Edmonds, 2017; Schmolke et al., 2010). The socio-economic model is a first attempt to include social norms in a quantitative (deterministic) model. It can promote the dialogue between academic disciplines and raise a discourse about how to build integrated models that represent the complexity of human decision-making (Delacámara et al., 2020; Edmonds, 2017; Epstein, 2008; Fischer and

Lindenmayer, 2007). A second reason why integrated models are not necessarily developed together with practitioners is that a model can raise new questions. This is conceivable particularly for complex interactions within coupled human-environment systems that can behave in unpredictable, nonlinear ways (Zvoleff and An, 2014). Hence, it would be myopic to restrict integrated models on existing questions by policy makers. In conclusion, each model type has advantages and disadvantages, but these are often relative to the stated objective (Lester, 2019). No model can simultaneously satisfy the quest for generality, realism and precision (Levins, 1966). I believe that both simple strategic models and integrated models for coupled human-environment systems that were used throughout this dissertation are essential to understand population dynamics potentially leading to biodiversity loss. Thus, management decisions should be based on rigorous ecological theory and verified by relevant mathematical models before being put into practice (De Angelis et al., submitted; De Lara and Doyen, 2008; Gurevitch and Padilla, 2004).

6.3 OUTLOOK

I want to conclude this dissertation by giving some perspectives for conservation. Let me distinguish between a scientific and a political perspective. The scientific outlook gives some directions for further investigations based on the models used in this dissertation. Much is to be done to obtain a comprehensive understanding of coupled human-environment (agricultural) systems. However, sufficient knowledge is available to put effective conservation into action (Harris et al., 2003). Therefore, I sum up some policy recommendations, mainly based on IPBES (2019).

6.3.1 *Scientific outlook*

Perspectives for further research based on each chapter of this dissertation is given within the respective discussion and is therefore not repeated at this point. I rather want to give an outlook on complementing the big picture of coupled human-environment systems. Agricultural landscapes as an example are approached in this dissertation from two directions: ecological and socio-economic systems are analyzed separately first. Then, a combined economic-ecological model is investigated. However, the coupled system does not yet consider feedbacks from the environmental to the human system, such as the dependence of agricultural yield on the presence of pollinators (Figure 6.1). In this dissertation, model complexity in this respect is missing but I can think of useful possibilities to extend the models: if social norms are included in farmers' decision-making, it will be interesting to investigate how the environmental state of the landscape alters the preference and behaviour of farmers for or against environmentally friendly land use (**Chapter 4**). Transitions towards conservation oriented attitudes through scheme participation are possible but a quantitative analysis is missing (Wilson and Hart, 2001).

In the coupled model in **Chapter 5**, long-term intensive land use does not alter the soil quality and hence the yield. However, it is known that intensive land use both reduces soil fertility and diminishes resilience, e.g. in the face of climate change (Lin, 2011;

Scotti et al., 2015). Moreover, the ecological effectiveness of action-oriented grassland schemes is doubtful (Sabatier et al., 2012). Hence, I suspect the model to overestimate both the ecological effect of the AES and the long-term crop yields. Accounting for the value of ecosystem services could be realized by replacing the grassland scheme e.g. by schemes that support diversified (agro-ecological) farming systems (Kremen, 2015). Agro-ecological systems rely on beneficial biodiversity for crop production (e.g., soil fertility, pest control, pollination, nutrient circulation) and are more resilient to cope with climate change (Fornara and Tilman, 2008; Garibaldi et al., 2016; Kremen, 2015). I suspect that such a scheme would be more successful in protecting biodiversity and make long-term yields less vulnerable to perturbations (if the opportunity of genetically modified crops is not considered). Further research could address whether, by adequate schemes, agriculture could be transformed towards a self-sustaining sector. Schemes could serve as a 'jumpstart' to promote adoption of sustainable agriculture and to provide financing programs to assist farmers with initial costs of transitioning (Kremen, 2015). It would be interesting to see how the dynamics change if the optimization problem for land-use decisions takes ecosystem services into account.

6.3.2 *Policy outlook*

The major current threats for biodiversity are recognized, and targets to reduce these threats are defined, e.g. in the Sustainable Development Goals of the United Nations (14 and 15 in particular). Suggestions how to reduce biodiversity loss are available based on scientific knowledge, e.g. in the IPBES reports. Environmental conditions are improved by maintaining protected areas, restoring natural ecosystems and improving the state of the habitat matrix, e.g. in urban areas (Bullock et al., 2011; Driscoll et al., 2013; Hanski, 2015; Kremen, 2015; Montoya et al., 2012). Biodiversity loss is reduced by sustainable wildlife management, regulation of exploitation and pest control (Hayward, 2011; IPBES, 2019). Negative effects of climate change are to be minimized (IPBES, 2019). Due to differences between species regarding their habitat requirements, structurally complex, well-connected habitats are reasonable (IPBES, 2019; Pardini et al., 2010). Strategies for wildlife-friendly agricultural land use in particular are inter alia: sustainable/ecological intensification, organic and agro-ecological practices (IPBES, 2019; Kremen, 2015; Schiefer et al., 2016). These practices could be enhanced through policy regulations, more results-based AES and by removal of distorting subsidies (Burton and Schwarz, 2013; IPBES, 2019).

None of the Aichi Biodiversity Targets 2020 have been fully met which shows that transforming the existing knowledge into action is lagging behind (Xu et al., in press). Despite a few achievements in improving the biodiversity status, efforts to address the underlying drivers and the reduction of direct pressures on biodiversity need to be strengthened (IPBES, 2019). A precautionary, integrated approach with close collaboration amongst institutions, managers, science and the public is required. Thereby, synergies and trade-offs between societal goals and nature conservation can be taken into account (Harris et al., 2003; IPBES, 2019). A mix of policies, including incentive and certification programs and environmental monitoring, is needed which replace detrimental policies and harmful subsidies (Butchart et al., 2010; Hanski, 2015; Hay-

ward, 2011; IPBES, 2019). Risks related to uncertainty and complexity during the transformation process towards a more sustainable life can be reduced through adaptive governance approaches that include ongoing reflection and learning (Butchart et al., 2010; IPBES, 2019; Kingsford et al., 2011).

Human well-being relies on ecosystem services not only to ensure economic welfare, food and energy supply. A variety of ecosystem functions such as regulation of climate, air quality and medicine are fundamental to preserve human life on Earth (GLP, 2005; IPBES, 2019). I fear that the self-interest in conservation is not yet recognized and therefore not sufficiently prioritized (Aspinall and Staiano, 2017; IPBES, 2019). If we want biodiversity conservation to succeed, we must not expect it to be achieved as a by-product of other policies but make efforts into a transformation of the existing system into a more sustainable one (Phalan et al., 2011a).

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ERKLÄRUNG ÜBER DIE EIGENSTÄNDIGKEIT DER ERBRACHTEN WISSENSCHAFTLICHEN LEISTUNG

Ich erkläre hiermit, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe. Die aus anderen Quellen direkt oder indirekt übernommenen Daten und Konzepte sind unter Angabe der Quelle gekennzeichnet.

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Die Arbeit wurde bisher weder im In- noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde vorgelegt.

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