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Multiple Attractors and Long Transients in Spatially Structured Populations with an Allee Effect

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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.

Keywords Coupled maps · Dispersal · Chaos · Fractal basin boundary · Crisis · Essential extinction

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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 (Dennis 1989; Courchamp et al. 1999; Stephens et al. 1999; Stephens and Sutherland 1999; Courchamp et al. 2008). 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 (Gruntfest et al. 1997; Amarasekare 1998; Gyllenberg et al. 1999; Kang and Lanchier 2011; Wang 2016; Johnson and Hastings 2018). 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 (Gyllenberg et al. 1993; Hastings 1993; Lloyd 1995; Gyllenberg et al. 1996; Kendall and Fox 1998; Earn et al. 2000; Yakubu and Castillo-Chavez 2002; Yakubu 2008; Faure and Schreiber 2014; Franco and Ruiz-Herrera 2015). A controversial question is whether chaotic behaviour of the population increases the probability of extinction (Thomas et al. 1980; Berryman and Millstein 1989; Lloyd 1995) 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 (Dennis 1989; Gruntfest et al. 1997; Amarasekare 1998; Courchamp et al. 1999; 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; Lloyd 1995; Kendall and Fox 1998; Yakubu and Castillo-Chavez 2002; Wysham and Hastings 2008; Yakubu 2008). 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 Sect. 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 Sect. 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 Sect. 4.

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.

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

$$f(x_t) = x_t e^{r\left(1 - \frac{x_t}{K}\right)\left(\frac{x_t}{A} - 1\right)}, \tag{1}$$

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 (Walters and Hilborn 1976; Turchin 1990; Estay et al. 2014). 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 (Schreiber 2003; Courchamp et al. 2008) may be more realistic but make visualization more difficult. However, our results do not depend on this choice.

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 Eq. (1). The patches are linked by dispersal:

$$
\begin{aligned}
x_{t+1} &= (1-d)f(x_t) + df(y_t), \\
y_{t+1} &= (1-d)f(y_t) + df(x_t),
\end{aligned}
\tag{2}
$$

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) correspond to iterating the map $F : C \to C$ given by $F(x, y) = ((1-d)f(x) + df(y), df(x) + (1-d)f(y))$.

3 Results

3.1 Dynamics Without Dispersal

In this section, we recap results from the local dynamics which are qualitatively similar to Schreiber (2003). System (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 orbit[1] for which $x_t = f^n(x_t)$ but $x_t \neq f^j(x_t) \;\; \forall \;\; j = 1, \ldots, n-1$; 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

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

distribution, extinction occurs with probability one (Schreiber 2003). This is shown in a bifurcation diagram with respect to r in Fig. 1a. The threshold r_{th} is marked with a dashed line. These properties of the local dynamics (1) can be formalized in a theorem (Appendix A).

Before turning towards the coupled model, we consider two isolated patches, that is, System (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 (1) delivers the equilibria of the uncoupled System (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 $\{p, f(p), \ldots, f^{n-1}(p)\}$ of period $n \geq 1$, the uncoupled map has $n+3$ stable periodic orbits given by the forward orbits of the following periodic points

$$\mathcal{P} = \{(0, 0), (0, p), (p, 0), (p, p), (p, f(p)), \ldots, (p, f^{n-1}(p))\}. \tag{3}$$

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

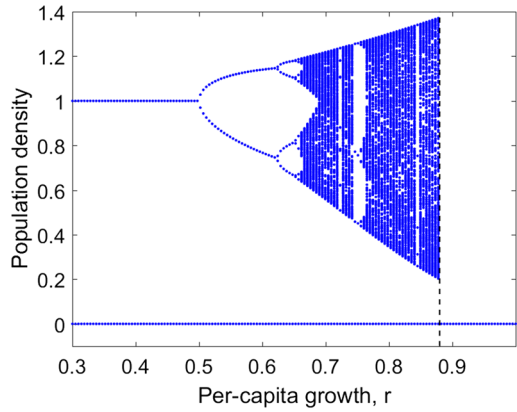## 3.2 Additional Attractors in the Coupled System

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, $\{p, f(p), \ldots, f^{n-1}(p)\}$, with period $n \geq 1$. Let U be an open neighbourhood of $\cup_{i=1}^{n} (f \times f)^i(\mathcal{P})$. Then, for $d > 0$ sufficiently small*
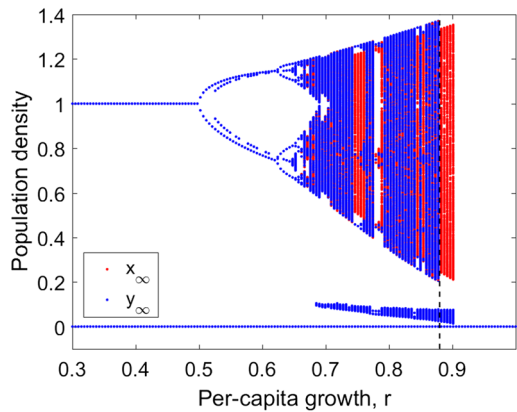
- *(i) System (2) has $n + 3$ distinct, linearly stable periodic orbits contained in U. Let G denote the union of these linearly stable periodic orbits.*
- *(ii) $C \backslash B$ has Lebesgue measure zero where $B = \{(x, y) \in C : \lim_{t \to \infty} \text{dist}(F^t(x, y), G) = 0\}$ is the basin of 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 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 $n + 3$.
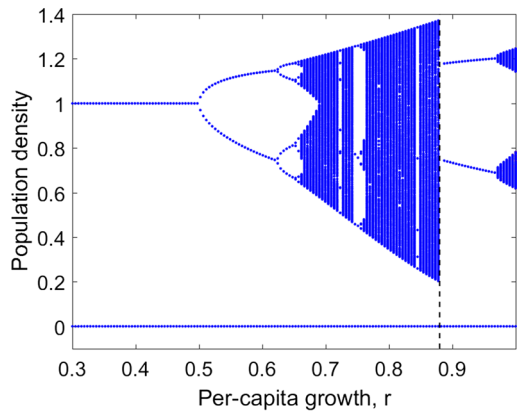
Fig. 1 Bifurcation diagram with bifurcation parameter r of **a** the dynamics of a single isolated population and of two populations in the coupled system with **b** dispersal fraction $d = 0.03$ whereby x_∞ (red) is hidden partially by y_∞ (blue) and **c** $d = 0.24$ whereby $x_\infty = y_\infty$; thus, 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 (Color figure online)

(a) Local dynamics

(b) Coupled system $d = 0.03$

(c) Coupled system $d = 0.24$

(a) Extinction

(b) Spatial asymmetry $y > x$

(c) Spatial asymmetry $x > y$

(d) In-phase 4-cycle

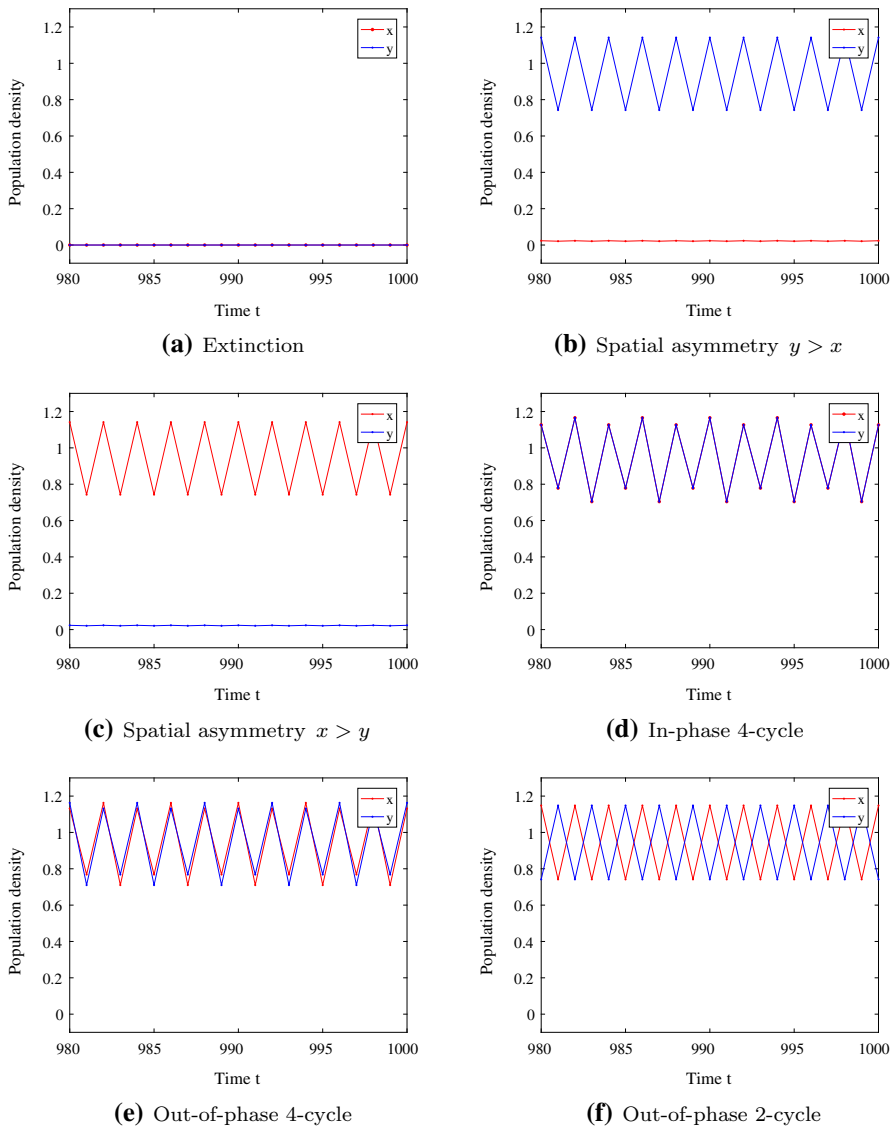**(e)** Out-of-phase 4-cycle

(f) Out-of-phase 2-cycle

Fig. 2 Time series of model (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** $x_0 = 0.38$, $y_0 = 0.58$ (Color figure online)

Consider System (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 Fig. 2. The extinction state in both patches is stable (Fig. 2a). The two attractors in Fig. 2b and c show periodic
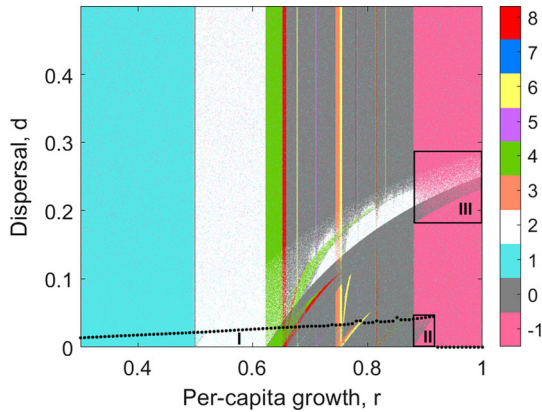
Fig. 3 Dynamical behaviour characterized by the periodicity, as a function of r and d. Labels of the colour bar give the periodicity of locally stable cycles. Periodicity 1 stands for a stable equilibrium (trivial or non-trivial), 0 for periods > 8 or chaos and -1 for extinction when $A < x_0 < 1 \lor A < y_0 < 1$. 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 (Color figure online)

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 (Fig. 2d) and only one out-of-phase 4-cycle (Fig. 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 (Fig. 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 Fig. 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 parameters, r and d. Figure 3 summarizes the dynamical behaviour that can be observed in the (r, d)-parameter plane for $0 < d < 0.5$ and $0.3 < r < 1$.

3.2.1 Multiple Attractors Due to the Allee Effect

In the case of weak dispersal (Fig. 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 (Fig. 3). Thus, spatial asymmetry can be conserved. Figure 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 (Fig. 3, above dotted curve). The asymmetric attractors disappear, and only extinction or persistence above the Allee threshold in both patches is possible. This is shown in Fig. 1c, where in comparison with Fig. 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.

3.2.2 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 Fig. 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 Fig. 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 are shown in Fig. 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; Yakubu and Castillo-Chavez 2002; Wysham and Hastings 2008; Yakubu 2008). 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 is discussed in Sects. 3.3 and 3.4.

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

3.3 Dispersal-Induced Prevention of Essential Extinction

In Sect. 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.

3.3.1 DIPEE Due to Spatial Asymmetry

For the moment, we only consider small dispersal $d < 0.05$ (Fig. 3, parameter region II). In this case, the coupling is sufficiently weak to observe different dynamics in both patches. Figure 4a, c, e shows the phase planes with nullclines[2] and sample orbits for different values of r. In Fig. 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 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 Fig. 4b. When the symmetric attractor disappears, its basin results in a fractal structure (Fig. 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 $(A, 0)$ (Fig. 4e). Almost all initial conditions lead to the only remaining attractor, the extinction state (Fig. 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 (Fig. 3, parameter region II). This result is emphasized in Fig. 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 Fig. 1b.

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[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 $y_{t+1} = y_t$.

(a) $r = 0.87 < r_{th}$

(b) $r = 0.87 < r_{th}$

(c) $r = 0.887 > r_{th}$

(d) $r = 0.887 > r_{th}$

(e) $r = 0.888 > r_{th}$
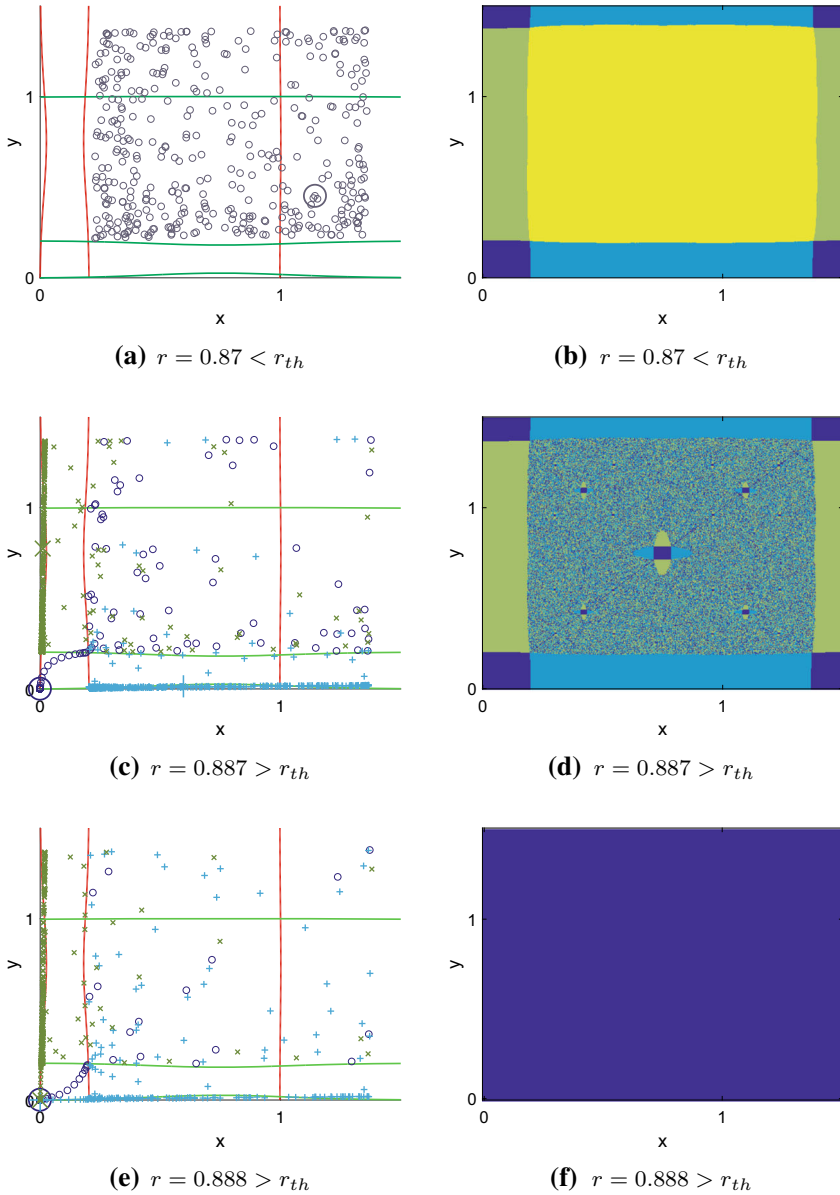

(f) $r = 0.888 > r_{th}$

Fig. 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 **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 (Color figure online)

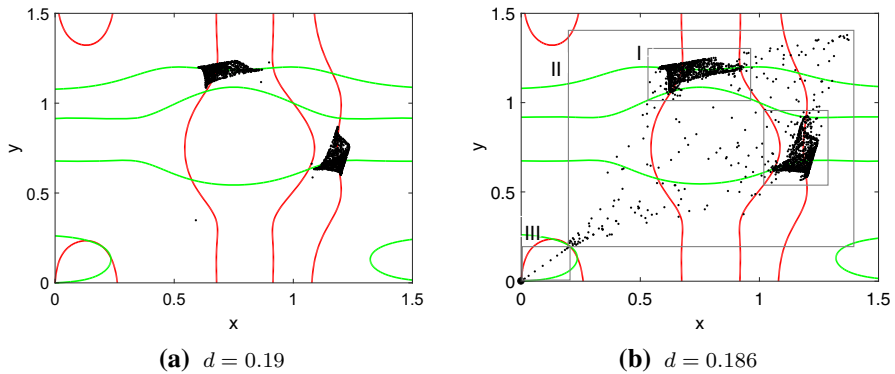**(a)** $d = 0.19$ **(b)** $d = 0.186$

Fig. 5 Phase planes with nullclines of the second iteration of System (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 $A = 0.2$, carrying capacity $K = 1$, $(A, A) < (x_0, y_0) < (\bar{A}, \bar{A})$, 1000 time steps, large symbol: final state (Color figure online)

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 $0.19 < d < 0.28$ (Fig. 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 (Fig. 5a). For values $r < r_{th}$, the symmetric out-of-phase dynamics coexist with a chaotic rhombus.[3] Initial 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 Fig. 7) and disappears, whereas the (approximately) out-of-phase dynamics persists. Figure 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 Fig. 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 Fig. 6a. When the chaotic rhombus disappears, the basins of attraction for symmetric attractors split into a fractal structure (Fig. 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

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[3] No obvious relationship between x_t and y_t (Kendall and Fox 1998); the attractor forms a rhombic structure.
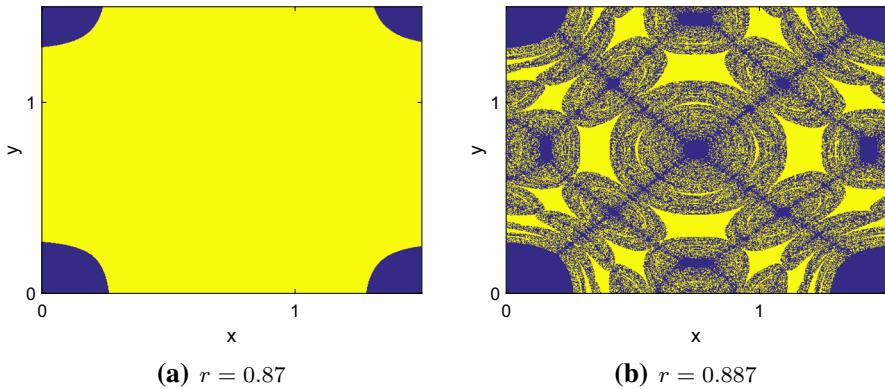
Fig. 6 Basins of attraction for $d = 0.23$ and **a** $r = 0.87$ and **b** $r = 0.887$. Blue indicates the extinction state, whereas yellow marks symmetric coexistence attractors. When r exceeds r_{th}, the basins change to a fractal structure. Allee threshold $A = 0.2$, carrying capacity $K = 1$ and 1000 time steps in all simulations (Color figure online)
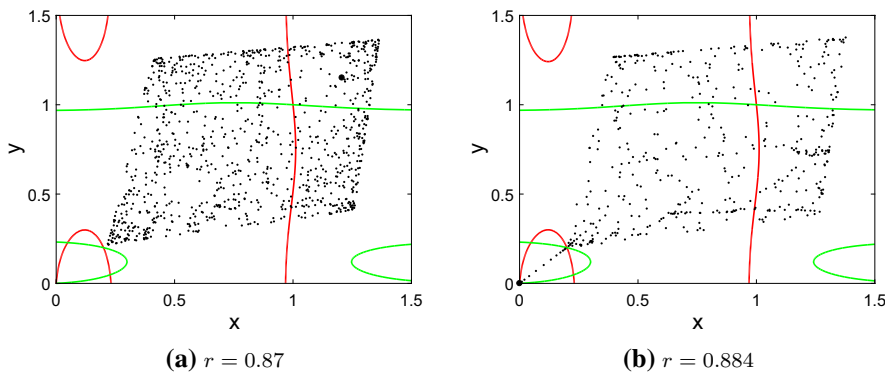

Fig. 7 Phase planes of the coupled system with $d = 0.1$ and **a** $r = 0.87$ and **b** $r = 0.884$, between which a boundary crisis eliminates the symmetric coexistence attractor. Allee threshold $A = 0.2$, carrying capacity $K = 1$, $(A, A) < (x_0, y_0) < (\bar{A}, \bar{A})$, 1000 time steps in both simulations, large symbols: final state. Nullclines in red and green, respectively (Color figure online)

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 No DIPEE

For $0.05 < d < 0.19$ and $d > 0.28$, dispersal cannot prevent essential extinction (Fig. 3, $r > r_{th}$, outside of regions II and III, pink parameter region). The symmetric attractor is a chaotic rhombus (Fig. 7a) which disappears after a boundary crisis for $r > r_{th}$ and thus leads to essential extinction for almost all initial conditions (Fig. 7b).
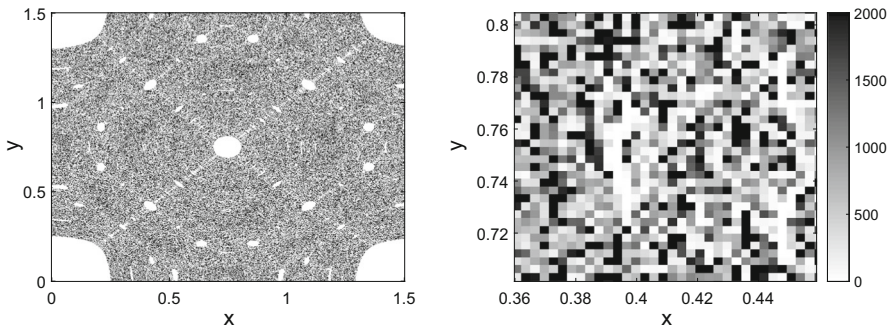
Fig. 8 Left: time to extinction for parameter values $r = 0.89$, $d = 0.186$ and initial conditions $x_0, y_0 \in (0, 1.5)$. Grey scale is chosen such that white means extinction after few time steps $t \approx 0$ and black means extinction at $t \approx 2000$ or later (see colour bar). The population is called extinct at time t when $x_t + y_t < 10^{-4}$. Right: enlarged section for selected initial conditions x_0, y_0

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 (Neubert 1997; Vandermeer and Yodzis 1999; Wysham and Hastings 2008; Bischi et al. 2016; Hastings et al. 2018). 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 shown in Figs. 4, 5 and 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 Fig. 5. The approximately out-of-phase attractor (I) in Fig. 5a undergoes a boundary crisis when d decreases and merges with the transient chaotic rhombus that is also shown in Fig. 7b. The two attractors disappear but are visible as ghosts (Fig. 5b, I and II). Finally, the population goes extinct (Fig. 5b, III). In contrast to Figs. 4 and 7, the nullclines of the second iteration[4] in Fig. 5 highlight the invariant set at which the boundary crisis occurs (intersections of green and red nullclines). Figure 8 presents the time to extinction for a range of initial population densities and the same parameters as used for Fig. 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 (Fig. 8). A steady-state analysis would not provide this information. From

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[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).
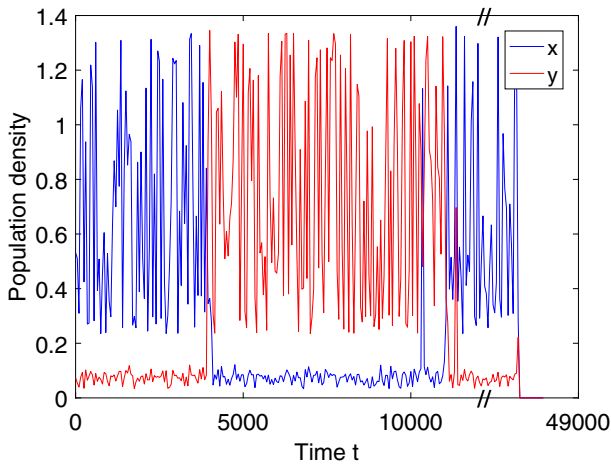
Fig. 9 Time series for parameter values $r = 0.898, d = 0.0415$ and initial conditions $x_0, y_0 = (0.07381, 0.53102)$. Time steps $t \in (12000, 45000)$ are hidden by a broken x-axis. Only every fifth value is plotted for better clarity (Color figure online)

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 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.

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 Knipl 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 density dependence 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 (Fig. 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).

Appendix A

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) $\lim\limits_{n \to \infty} f^n(x) = 0$ $\forall x \notin [a, b]$

(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 $\lim\limits_{n \to \infty} f^n(x) = 0$ $\forall x \notin [A, A^*]$.

– Essential extinction: If $f(M) < A$, then $\lim\limits_{n \to \infty} f^n(x) = 0$ for Lebesgue almost every x.

– Chaotic semistability: If $f(M) = A$, then the dynamics of f restricted to $[A, A^*]$ are chaotic and $\lim\limits_{n \to \infty} f^n(x) = 0$ $\forall x \notin [A, A^*]$.

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

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

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

(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 $a \in (0, A)$. $\lim\limits_{x \to \infty} f(x) = 0$ 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:

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

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

– $\lim_{x \to \infty} q_2(x) = \infty$.

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

Appendix B: Proof of Theorem 1

To prove the theorem, let $\widetilde{F}(x, y) = (f(x), f(y))$ 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 $\mathcal{O} = \{p, f(p), \ldots, f^{n-1}(p)\}$ 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 van 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 $\widetilde{F}$ is an Axiom A endomorphism (Przytycki 1976, p. 271): the derivative of $\widetilde{F}$ is non-singular for all points in the non-wandering set $\Omega(\widetilde{F}) = \{(x, y) \in C : \text{for every neighbourhood } U \text{ of } (x, y), \widetilde{F}^t(U) \cap U \neq \emptyset \text{ for some } t \geq 1\}$, $\Omega(\widetilde{F})$ is a hyperbolic set, and the periodic points are dense in $\Omega(\widetilde{F})$. Przytycki (1976, 3.11–3.14 and 3.17) imply that (i) $\Omega(\widetilde{F})$ decomposes in a finite number of invariant sets $\Omega^1(\widetilde{F}), \ldots, \Omega^m(\widetilde{F})$ and (ii) maps sufficiently C^1 close to $\widetilde{F}$ are Axiom A endomorphisms whose invariant sets $\Omega^i(F)$ are close to $\Omega^i(\widetilde{F})$. In particular, property (ii) implies that $F(x)$ is an Axiom A endomorphism provided that $d > 0$ is sufficiently small. The invariant sets $\Omega^i(\widetilde{F})$ for $\widetilde{F}$ correspond the linearly stable periodic orbits defined by $\mathcal{P}$, and products of the hyperbolic repellers for f and the linearly stable periodic orbits of f. Without loss of generality, let $\Omega^i(\widetilde{F})$ for $1 \leq i \leq n + 3$ correspond to the linearly stable periodic orbits of $\widetilde{F}$ and $\Omega^i(\widetilde{F})$ for $i > n + 3$ correspond to the saddles and repellers of $\widetilde{F}$. 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, Sharkovsky (1964) 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 $\cup_{i>n+3}\Omega^i(\widetilde{F})$ of $\widetilde{F}$ 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.

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