

Resilience in a Two-Population System: Interactions between Allee effects and connectivity

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Abstract Resilience in ecosystems and resistance to regime shifts has been a major focus in ecological research. How migration and general network dynamics affect the resilience of populations or induce regime shift cascades is a particularly challenging open question in theoretical ecology. We focus on regime shifts in populations with variable-strength Allee effects to demonstrate the effect of migration on resilience in two-population systems with critical transitions. The result is a mathematical model that justifies the assumption that resilience can be averaged across connected populations and suggests several management strategies to either avoid or induce regime shift cascades.

Keywords resilience · regime shifts · migration · Allee effect

1 Introduction

The major mathematical focus of studies of regime shifts has been on aspects of saddle node or transcritical bifurcations. From an ecological standpoint, the simplest system with the potential to exhibit a regime shift is a population with an Allee effect (Courchamp et al 2008; Taylor 2012). In a population with an Allee effect, the per capita growth rate increases as the population size increases at low population levels (but still decreases at high population levels). If the population growth rate is always positive at low levels, the Allee effect is called

weak; if there are population levels below which the population growth rate is negative, the Allee effect is called strong. Thus, if there is a strong Allee effect, then there is a survival threshold.

Transitions between the strong and weak Allee effects therefore provide the simplest example of a transcritical bifurcation and regime shift in ecology. To examine the effects of external environmental change causing regime shifts, a model that, as a function of its parameters, can either exhibit a strong or weak Allee effect is needed. A deteriorating environment changes a weak Allee effect into a strong one. Further deterioration of the environment then leads to a *fatal* Allee effect, a system where the population growth rate is always negative; there is no threshold above which population growth rate is positive. The transition between the strong Allee effect and fatal Allee effect yields a simple example of a saddle node bifurcation. The case of a single population exhibiting this kind of behavior would be easy to analyze.

Of greater interest, and implicit in many studies of regime shifts, is how regime shifts will cascade through an ecosystem. A major concern is how crossing a threshold in one population affects other interacting populations. A simple system of interacting populations is two local populations connected by movement of individuals. In the simplest case movement is modeled by passive diffusion. In this paper, we look at a two-population model to examine how deterioration of the environment in one site affects the dynamics in the other site. In particular, we look for “rescue effects” where a population is rescued from extinction by a neighboring population, as in (Amarasekare 1998) where a model with two populations connected by dispersal, each having a strong Allee effect is analyzed. What the study (Amarasekare 1998) does not consider is how the dynamics of

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this system changes as dispersal and local population dynamics are varied so the system undergoes one or more saddle-node bifurcations corresponding to what is known as critical transitions. This kind of analysis requires a different underlying model where the local dynamics can change from weak Allee effect to strong Allee effect to certain local extinction as a parameter representing habitat quality is varied. The two-patch model we study is thus one of the simplest ones that can exhibit cascading effects where a critical transition in one population can affect another population.

In order to compare the “resilience” of populations in either the monostable (weak Allee effect) or bistable (strong Allee effect) regime, we consider a slightly different definition of ecological resilience in view of (Holling 1973). We define the resilience of a population to be the amount of perturbations that a population can tolerate without either shifting to the extinction state or entering the attracting domain of the extinction state. In the monostable case, this is the magnitude of the positive stable fixed point, whereas in the bistable case, this is still the classic definition of resilience - the distance between the positive stable state and the unstable threshold state.

Although our analysis is deterministic, the approach we use is only a first step towards understanding the dynamics of coupled stochastic populations. Given both the ubiquity of Allee effects and the complexity of the dynamics we uncover, the deterministic results already provide important insights into the dynamics of coupled populations in a changing world. In this paper, we will lay the foundations for how neighboring populations with similar dynamics undergo regime shifts with respect to one another, and how the resilience of an ecosystem is either bolstered or weakened by its connectivity.

2 Model

Consider a population with the potential to exhibit either a strong Allee effect, a weak Allee effect, or a fatal Allee effect, depending on some quality in the environment. In the strong Allee effect regime, the population exhibits alternate stable states - survival and growth up to a carrying capacity or extinction. Let the average of its carrying capacity and Allee threshold be the quantity γ (units of individuals) and let the radius of the attractive basin of the carrying capacity stable state be the quantity $\sqrt{\beta}$. Then the carrying capacity of the population will be $\gamma + \sqrt{\beta}$ individuals and the Allee threshold will be $\gamma - \sqrt{\beta}$ individuals. With intrinsic growth rate r , we have a model for population growth

with a strong Allee effect (see (Edelstein-Keshet 2005)).

$$\dot{X} = -rX(X - \gamma - \sqrt{\beta})(X - \gamma + \sqrt{\beta}) \quad (1)$$

or

$$\dot{X} = rX(\beta - (X - \gamma)^2). \quad (2)$$

When $\beta = 0$, the carrying capacity and Allee threshold coalesce into one state, so for $\beta < 0$, only the extinction state is possible (fatal Allee effect regime). For $0 < \beta < \gamma^2$, the system is in the alternate state regime, with the Allee threshold separating the attracting basins of the carrying capacity state and extinction state (strong Allee effect regime). When $\beta = \gamma^2$, the Allee threshold crosses through the extinction state, so for $\beta > \gamma^2$, the only possible stable equilibrium is the carrying capacity state (weak Allee effect regime). Since β is the distance-squared between the carrying capacity or Allee threshold from the average of the two, it can be thought of as the measure for the quality of the environment for the population. The larger the value of β , the lower the Allee threshold and the larger the attractive basin of the carrying capacity state, and thus the higher quality of the environment. When β is sufficiently high, the Allee effect is weak, and when β is negative, the Allee effect is fatal. We can nondimensionalize the system to effectively set $r = 1, \gamma = 1$, so that the nondimensional model is

$$\dot{X} = X(\beta - (X - 1)^2), \quad (3)$$

where the model now operates on a nondimensional time and X is a nondimensional measure of population size.

The transitions between strong, weak, and fatal Allee effect regimes as β is varied in Equation (3) are summarized in the bifurcation diagram in Figure 1. The main question of interest is how spatial coupling alters regime boundaries and decreases system resilience through regime shifts. We look at a simple two-population model with coupling via symmetric passive diffusion. The model equations for this two population system are

$$\dot{X}_1 = X_1(\beta_1 - (X_1 - 1)^2) + D(X_2 - X_1) \quad (4)$$

$$\dot{X}_2 = X_2(\beta_2 - (X_2 - 1)^2) + D(X_1 - X_2), \quad (5)$$

where subscripts denote location. Noting the bifurcation structure in the single population model, we examine the effects of varying just the quality parameter β_i between the two populations. We assume that r_i and γ_i are equivalent in the two populations so that the nondimensionalization is the same, and focus only on the regime shifts in β_i . We can answer many questions through this analysis, e.g. what happens if X_1 is past its

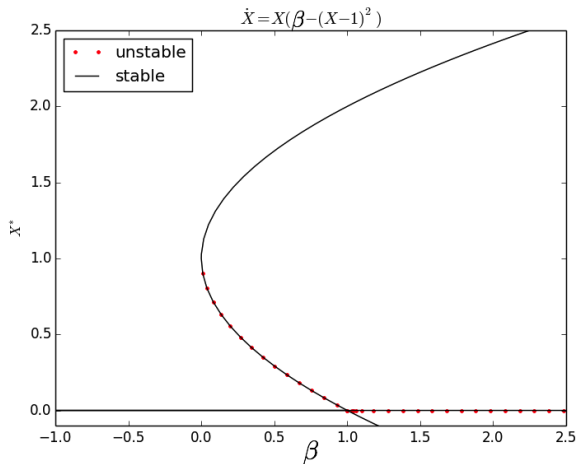


Fig. 1: The bifurcation diagram for equation (3) with bifurcation parameter β . Note the three regimes: $\beta < 0$ Fatal Allee Effect/ Extinction; $0 < \beta < 1$ Strong Allee Effect / Bistability; $\beta > 1$ Weak Allee Effect.

Allee Effect	Coupled Regime Cases		
	Strong	Weak	Fatal
Strong	1	2	3
Weak		5	4
Fatal			6

Table 1: The six possible cases of pairings that will be analyzed in the paper, e.g., Case 1 is a population with a strong Allee effect coupled with a population with a strong Allee effect, etc.

tipping point in the extinction regime ($\beta_1 < 0$) and X_2 is in the bistable regime ($\beta_2 > 0$)? We also investigate how the magnitude of migration affects the resilience of the system.

3 Analysis

We look at the effects of varying the parameters that determine the local environmental quality β_i between the two populations, and the effects of the migration parameter D on the resilience of the system. The analysis can be broken down into six essential cases - each case consisting of a pair of regimes for the two populations, e.g. fatal Allee effect regime in pop. 1 paired with strong Allee effect in pop. 2. The cases are summarized in Table 1.

We argue that cases 5 and 6 are not mathematically or ecologically interesting. Two populations with fatal Allee effects coupled together will remain extinct, so case 6 is trivial. Similarly, two populations with weak Allee effects coupled together symmetrically will remain

at a stable equilibrium (not necessarily the respective carrying capacities, since dispersal may change numerical values), so case 5 is not surprising. The remaining cases have potential for interesting dynamics and important ecological effects, so we will focus on these for the analysis. Case 1 has been analyzed in (Gruntfest et al 1997), so we will briefly summarize the results here for completion.

3.1 Case 1: Strong-Strong Pairing

In this case, both populations X_1 and X_2 are in their respective bistable regimes ($0 < \beta_1, \beta_2 < 1$).

Without any migration, the two populations exhibit independent dynamics: each population is either in its high state or extinction state, separated by the respective Allee thresholds.

With the introduction of a small amount of migration, the dynamics aren't changed qualitatively, but the population levels at the various states are altered quantitatively.

Increasing the migration further removes all the unstable states of the paired model except one, leading to a bistable regime with either extinction for both populations or high level persistence for both.

Thus the dynamics of the two populations become intertwined, and the system behaves like a single population in a strong Allee effect regime. See (Gruntfest et al 1997) for a more thorough analysis of the dynamics of this case.

3.2 Case 2: Weak-Strong Pairing

In this case, population 1 (X_1) is in its bistable regime ($0 < \beta_1 < 1$), and population 2 (X_2) is in the weak Allee effect regime ($\beta_2 > 1$). The effects of migration on X_1 can be seen in the bifurcation diagram in Figure 2. With no migration ($D = 0$), the dynamics are independent and X_1 is either at carrying capacity or extinct, and X_2 is at carrying capacity. With any amount of migration, the bistable population's extinction state is supported at a low level by the more resilient population, see $0 < D < 0.015$ in Figure 2. As migration increases, the possibility for bistability in population 1 is removed, and both populations are in a weak Allee effect regime, see $D > 0.015$ in Figure 2. This suggests that with a significant level of migration, the flow of migrants from X_2 to X_1 is high enough to always overcome the Allee threshold of X_1 ; effectively, this changes the Allee effect on X_1 from strong to weak. The reciprocal effect on X_2 throughout this shift in D is the introduction of a short-lived bistable regime corresponding to

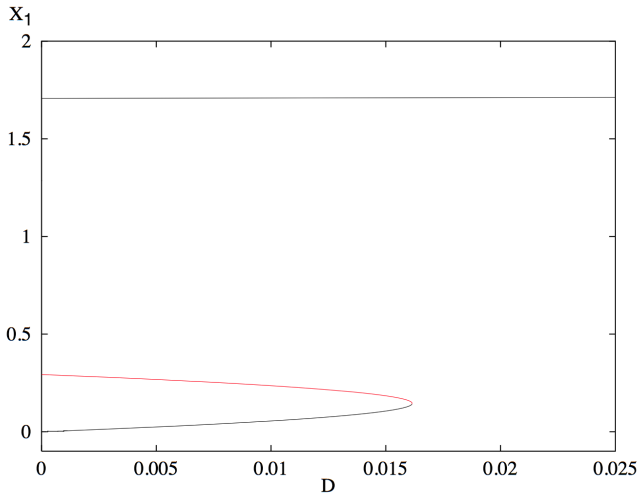


Fig. 2: Bifurcation diagram for X_1 and D in case 2 for $\beta_1 = 0.5$, $\beta_2 = 1.5$. Black lines indicate stable states, red indicates unstable. Note $X_1 = 0$ is only a stable state for $D = 0$.

the bistable regime in X_1 shown in Figure 2. In other words, bistability in X_2 exists for D from roughly 0 to 0.017, a very narrow parameter range, and the difference between the bistable X_2 states is roughly 0.2%. These two states would essentially look like a single stable state around $X_2 \approx 2.225$, so the bifurcation diagram was not presented here.

3.3 Case 3: Strong-Fatal Pairing

This case exhibits the richest dynamics, and so will be the bulk of the analysis. In this case, population 1 (X_1) is in the fatal Allee effect regime ($\beta_1 < 0$), and population 2 (X_2) is in the strong Allee effect regime ($0 < \beta_2 < 1$). If β_1 and β_2 , the habitability parameters of the two environments, are held constant, then increasing the magnitude of the migration between the two sites can bring population 1 out of the fatal Allee effect regime. This is illustrated in the bifurcation diagram in Figure 3(a). Increasing D past 0, we see an immediate introduction of a new, low-magnitude stable state for X_1 . In Figure 3(a), this state persists from $D = 0$ to $D \approx 0.18$. Increasing the migration further yields a bistable regime, between $D \approx 0.10$ and $D \approx 0.18$ in Figure 3(a). Further increasing D yields a strong Allee effect regime in X_1 , see $D > 0.18$ in Figure 3(a). The reciprocal effect on X_2 throughout this shift in D can be seen in Figure 3(b). For small D , there is a decrease in the magnitude of the high stable state. As the bistable regime appears in X_1 around $D = 0.10$, a corresponding bistable regime emerges in X_2 . The

lower stable state corresponds to supporting X_1 at the low state, and the higher stable state corresponds to supporting X_2 (and being reciprocally supported) at the high state. Note that both stable states for X_2 are greater than 1 here, so the risk of extinction is not high. Once the weak Allee effect has been established in X_1 , only the higher stable state of X_2 persists, see $D > 0.18$ in Figure 3(b).

If the habitability parameter β_2 for population 2 is varied (but remains within the bounds for the bistable regime for the single-population model, $0 < \beta_2 < 1$), we observe qualitatively different behavior for the two-population model. We explore the effects of varying β_2 and D in the stability diagram in Figure 5.

Figure 5 shows that as β_2 and D are varied, there are four distinct regimes that appear in the system for $\beta_1 = -0.04$. Regime I corresponds to a single equilibrium of the system: extinction of both X_1 and X_2 . Regime II corresponds to a bistable regime, where one possible stable state is a high level of both X_1 and X_2 , and the other possible stable state is extinction, with a single unstable equilibrium between the two states. Regime III is an alternate state regime with the two stable states as in Regime II and also a third state: a high level of X_2 and low level of X_1 . Regime IV is a bistable regime of either a high level of X_2 and low level of X_1 or extinction of both populations.

Transitioning out of Regime III into one of the other regimes is the most interesting scenario. The downward-sloping boundary between Regime III and Regime IV in Figure 5 signifies that as the fitness of population 2's habitat, β_2 , decreases, the level of migration needed to sustain the high level for X_1 is increased, so only the low level of X_1 is sustainable. On the other hand, the downward-sloping portion of the II-III boundary shows that the migration can become so large that the high level of X_2 is only sustainable alongside a high level of X_1 . Similarly, the portion of the boundary to the right of the cusp shows that the more habitable site 2 becomes (β_2 increases), the less migration is needed for X_1 to exceed its Allee threshold and grow near to its carrying capacity. The upward-sloping portion of the II-III boundary to the left of the cusp shows that as site 2 becomes less habitable (β_2 decreases), then less migration is necessary to remove the possibility of X_2 surviving with only a low level of X_1 nearby.

Since crossing the II-III boundary removes the low X_1 , high X_2 stable state, what happens if the system is at that state as it disappears? The answer depends on which side of the cusp in Figure 5 the transition occurs over. If the system crosses from Regime III into

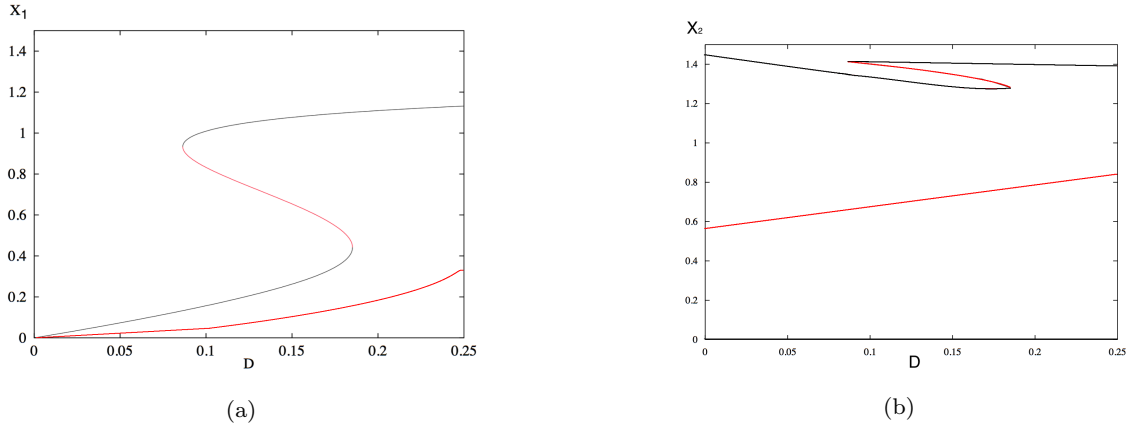


Fig. 3: Bifurcation diagrams for the strong-fatal pairing with $\beta_1 = -0.04$, $\beta_2 = 0.2$ for: (a) X_1 and D ; (b) X_2 and D . Black lines indicate stable states, red indicates unstable. Note that 0 is always a stable state for both X_1 and X_2 . Note that transitioning from regime III to II ($D < 0.17 \rightarrow D > 0.17$) can yield growth up the high/high stable state. This illustrates the effect of crossing the II/III boundary to the right of the cusp in Figure 5.

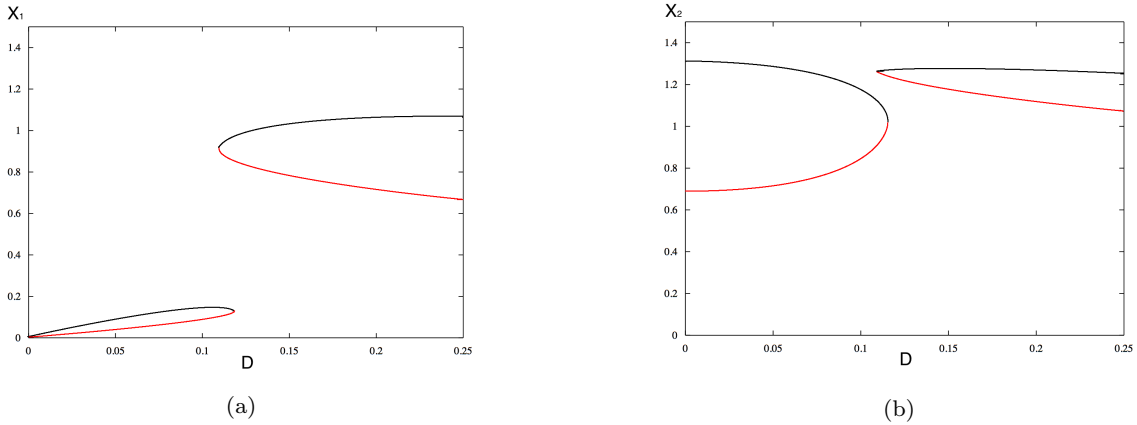


Fig. 4: Bifurcation diagrams for the strong-fatal pairing with $\beta_1 = -0.04$, $\beta_2 = 0.1$ for: (a) X_1 and D ; (b) X_2 and D . Black lines indicate stable states, red indicates unstable. 0 is always a stable state for both X_1 and X_2 . Note that transitioning from regime III to II ($D < 0.12 \rightarrow D > 0.12$) can lead to dual extinction. This illustrates the effect of crossing the II/III boundary to the left of the cusp in Figure 5.

Regime II through the right side of the cusp, then the system will move towards the high X_2 , high X_1 stable state; this transition is illustrated in Figure 3. Note that since X_1 has effectively gained a strong Allee effect through this pairing, it has also gained an unstable Allee threshold state, and so this transition corresponds to the X_1 Allee threshold colliding with the current system state, yielding an attraction to the high X_1 , high X_2 state. However, if the system crosses from Regime III into Regime II through the left side of the cusp, then the system will move towards extinction of both populations. This transition is illustrated in Figure 4. This corresponds to the X_2 Allee threshold colliding with the current system state, yielding an attraction to the

extinction case. The cusp in Figure 5 thus corresponds to both thresholds colliding with the low/high state.

Another question arises, is there a threshold of environmental quality of site 1 below which any survival for population 1 is impossible? As β_1 is decreased, the D - β_2 parameter regime yielding three stable states (regime III in Figure 5) shrinks until the saddle-node boundary between regimes II and III on the right of the cusp collides with the saddle-node boundary between regimes III and IV, around $\beta_1 = -0.13$, see Figure 6(a). This yields two distinct parameter regimes, with a single boundary between the two, as shown in Figure 6(b). The left regime (Regime I) is extinction, and the right regime (Regime II+IV) is bistable. The bistable regime consists of extinction and a high-magnitude X_2 , variable-

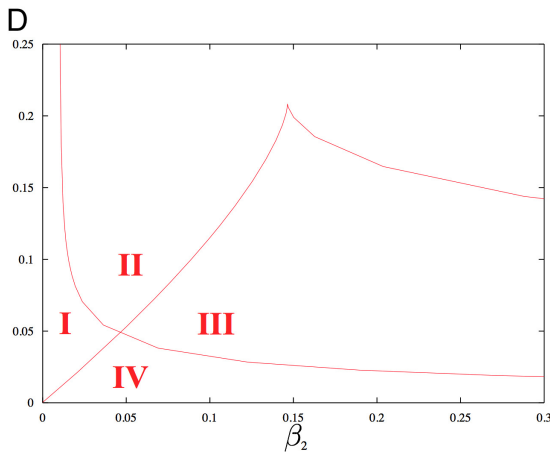


Fig. 5: Stability diagram for the strong-fatal pairing for D and β_2 , with $\beta_1 = -0.04$. The stable states (X_1/X_2) of each regime: (I) 0/0; (II) 0/0, high/high; (III) 0/0, low/high, high/high; (IV) low/high, high/high.

magnitude X_1 stable state. X_1 varies from low to high magnitude, reflecting its level in regions II or IV in the previous parameter regime in Figure 6(a). This transition can be seen in the bifurcation diagrams in Figure 7. In Figure 7(a), β_2 is held constant and migration D is increased, leading to a steady increase in the stable population level of X_1 . In Figure 7(b), the reciprocal effect on X_2 is shown. Comparing Figure 7 with Figure 3, observe that the stable population levels of X_1 and X_2 are similar to their respective comparisons, and the loss of the unstable states is evident.

3.4 Case 4: Weak-Fatal Pairing

In this case, population 1 (X_1) is past its tipping point in the extinction regime ($\beta_1 < 0$), and population 2 (X_2) is in the weak Allee effect regime ($\beta_2 > 1$). This case is quite similar to case 3 in the supportive effect on the less resilient population, but differs in that the more resilient population has no Allee threshold for the connection to effectively raise or lower. Thus the dynamics are exactly the same as in the righthand-side of Figure 5; the system is either in Regime II, III, or IV. Regime II corresponds to an alternate state regime, where one possible stable system state is a high level of both populations, and the other possible state is extinction of both populations. Regime III corresponds to a regime with three alternate states, where one possible stable system state is a high level of X_2 (the population with a weak Allee effect) and a low level of X_1 (the population with a fatal Allee effect), and the other two possible stable system states are the same as the possible states of Regime II. Regime IV corresponds to an

alternate state regime, where one possible stable system state is a high level of X_2 and low level of X_1 , and the other state is extinction of both. Just as in the previous case, Regime III can be eliminated at some negative β_1 value as in Figure 6, which happens as Regimes II and IV combine to form a single alternate state regime, with extinction as one state and a high-level X_2 , gradient-level X_1 as the other state. Another distinction from the previous case is that the transition from Regimes III to II from the mixed state always leads to the high X_2 , high X_1 state, since the transition always occurs to the right of the cusp in figure 5.

3.5 Analysis of Resilience

Connecting the two populations, in any Allee effect regime pairing, has a resilience-averaging effect. The less resilient population is supported by the more resilient, boosting extinction states up to low-level states and moving Allee thresholds closer to zero, effectively increasing the resilience of the less resilient population. On the other hand, the more resilient population is “dragged down” by the less resilient, lowering the magnitudes of its high-level states and moving its Allee thresholds closer to the high-level state, effectively lowering the resilience of the more resilient population.

As Figure 8 shows, coupling population X_1 to a more resilient population X_2 shifts the saddle-node bifurcation of its high-level and Allee threshold states towards negative β_1 values and replaces the transcritical bifurcation of its Allee threshold and low-level states to a saddle-node bifurcation, which also moves in the negative β_1 direction. The transcritical to saddle node bifurcation shift and the leftward shift of the saddle node bifurcations is illustrated in Figure 8. This is a clear increase in resilience, as the catastrophic shift to a fatal Allee effect regime is pushed away and the weak Allee effect regime (and its conference of resilience) encroaches into the strong Allee effect parameter space. On the other hand, coupling X_1 to a less resilient population X_2 has the opposite effect on resilience. The transcritical bifurcation remains intact and shifts towards greater β_1 values, and the saddle node bifurcation shifts towards greater β_1 values as well. This is a clear loss of resilience, as the catastrophic shift to a fatal Allee effect regime is pulled into what was previously a strong Allee effect regime, and the transition to the weak Allee effect regime (and its conference of resilience) is pushed away.

As the migration rates and pairings are varied, there are many possible regimes for the two-population system, which we summarize in Table 2. In Table 2, 0/0 is used to indicate the regime where both populations

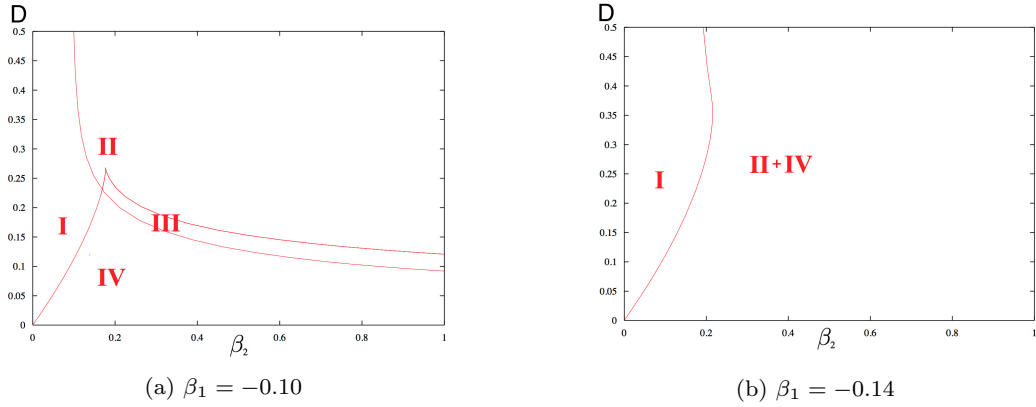


Fig. 6: (a) Stability diagram for the strong-fatal pairing for D and β_2 , with $\beta_1 = -0.10$. Note how regime III shrinks in size as β_1 decreases as compared to Figure 5.

(b) Stability diagram for case 3 for D and β_2 , with $\beta_1 = -0.14$. Note the collision of the Regime III-IV boundary (compared with Figures 5, 6a) with the II-III boundary as β_1 is decreased. Regime III has disappeared and regimes II and IV have combined to form a continuous gradient of X_1 population level reflecting the previous regime values.

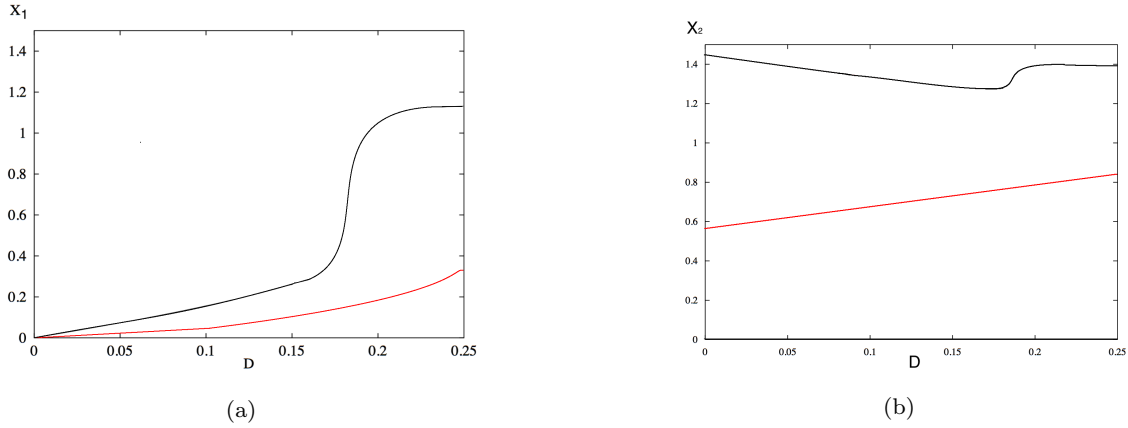


Fig. 7: Bifurcation diagrams for the strong-fatal pairing with $\beta_1 = -0.14$, $\beta_2 = 0.2$ for: (a) X_1 and D ; (b) X_2 and D . Black lines indicate stable states, red lines indicate unstable states. 0 is always a stable state for both X_1 and X_2 . Compare with Figure 3 to observe the loss of the unstable states and the similar stable population levels of X_1 and X_2 .

have only extinction as a steady state, high/low indicates the regime where population 1 is at its high-density near-carrying capacity state while population 2 is at its low-density supported state, and so on.

4 Discussion

Our analysis of two coupled populations with Allee effects of different kinds shows interesting ecological and mathematical outcomes. We express the ecological effects in terms of resilience, where clearly the interesting case is the behavior of the system when there is a strong Allee effect in one location. The structure of the dynamics with two strong Allee effects has been examined previously (Amarasekare 1998), but we obtain

new behaviors and new ecological consequences by asking how the system responds as parameters are varied which change the connectivity, the strength of the Allee effects, and even the characteristics of the Allee effects from weak to strong to fatal.

We should emphasize that pairings that include what we call a fatal Allee effect may be of particular interest. Reductions in environmental quality (including anthropogenic effects like harvesting or other changes) that in our model change the dynamics within one population from a strong Allee effect to a fatal Allee effect correspond exactly to the most well studied critical transition (saddle-node bifurcation) that is typically studied in the context of early warning signs (Scheffer 2009). So our asking here how changing one population from

Table 2: Possible states in various coupled systems.

	Monostability	Bistability	Tristability	Quadstability
Fatal-Fatal	0/0	-	-	-
Weak-Weak	high/high	-	-	-
Weak-Fatal	-	high/high, 0/0 high/low, 0/0	high/high, high/low, 0/0	-
Strong-Fatal	0/0	high/high, 0/0 high/low, 0/0	high/high, high/low, 0/0	-
Weak-Strong	high/high	high/high, high/low	-	-
Strong-Strong	-	high/high, 0/0	-	high/high, high/low, low/high, 0/0

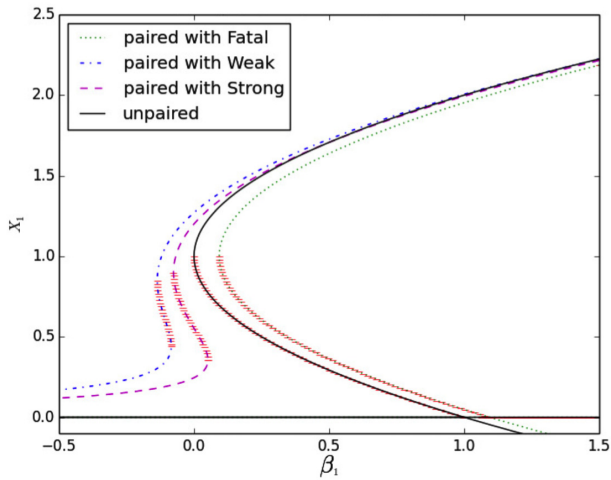


Fig. 8: The shifted bifurcation diagrams for two coupled populations in various regimes with $D = 0.1$ with population in location 1, X_1 , shown; note the leftward shift of the saddle-node bifurcation for the pairings to Strong and Weak regimes and the loss of the transcritical bifurcation for X_1 for the pairings to Strong and Weak regimes of X_2 . For the coupling to the Strong and Weak paired regimes, X_2 was at its high-level stable state, and for the coupling to the Fatal paired regime, X_2 was at its low-level stable state.

a strong to fatal Allee effect affects the whole system is asking what happens when the underlying dynamics in a single (isolated) population undergo a critical transition. Clearly, the consequences will depend on how far past the critical transition point the single patch is, the connectivity level, and the dynamics in the other patch, as we elaborate below.

The underlying mathematical dynamics are of surprising complexity as we describe below, so we also sought some simplifying descriptions in terms of resilience. Although our analysis here is completely deterministic, we do describe some implications for considering management in the context of critical transitions, since we uncover different kinds of possible transitions.

We next describe how resilience in terms of the size of basins of attraction to desirable states depends on parameters. We then consider, based on the deterministic analysis here, what the likely effects of stochasticity would be. Finally, we emphasize the appearance and consequences for management of the cusps in Figure 4, which imply that increases (or decreases) of habitat quality can have surprising effects.

This model and analysis shows that this definition of resilience is effectively averaged across spatial locations with variable-Allee effect populations. For systems with the possibility of sharp transitions between bistable regimes and monostable regimes, spatial connections smoothen the transitions and provide a wider parameter window for resilience in the bistable regime. This effect is best demonstrated in Figure 8. Coupling a population with a non-fatal Allee effect population immediately breaks the symmetry in the lower transcritical bifurcation, yielding a second saddle node bifurcation and effectively reducing the Allee threshold parameter window. Thus this immediately confers an increase in resilience for the population, as the probability that it goes extinct due to a disturbance is significantly lessened outside of the Allee threshold regime ($0 < \beta < 1$ in the uncoupled case) (Taylor 2012). The resilience-averaging effect can be seen clearly in Figure 8, as coupling a population to a weak or strong Allee effect population shifts the carrying capacity/Allee threshold saddle node bifurcation leftwards, effectively increasing the resilience of the population. On the other hand, the more resilient population has its saddle node shifted rightwards, effectively decreasing its resilience.

Environmental or demographic stochasticity may weaken these results, however, since it could make the novel low/high stable state unviable in reality. Further work could include stochasticity in the model to see how the sharp bifurcation diagram shifts in Figure 8 are smoothed or blurred. Not only must we better understand environmental processes that quantitatively affect parameters underlying the resilience of particular population states (Beisner et al 2003), but we must also understand the spatial distribution and connectivity of

the population network in order to better capture its resilience. To build on work on similar critical transitions in continuous-space population networks, the resilience-averaging effect of spatial coupling should be incorporated into the prediction of the Maxwell point for regime shift cascades (Bel et al 2012). Populations are more effectively modeled through a discrete spatial distribution, which necessarily has sharp state boundaries between sites.

Notable again in this analysis is the fact that the generic structure of the bifurcation diagram for the uncoupled population is left intact by the coupling. The carrying capacity/Allee threshold saddle node bifurcation is only shifted left or right in parameter space, but it remains detectable by standard warning signals such as critical slowing down (Boettiger et al 2013). Similarly, the Allee threshold/extinction transcritical bifurcation is replaced by a saddle node bifurcation, so it also remains detectable by critical slowing down (Scheffer et al 2015). Thus the underlying dynamics of this two-population model lies in the standard class of detectable critical transitions, though warning signals for pairs of saddle nodes has not yet been thoroughly investigated. The usefulness of spatial critical slowing down as a warning signal (Dai et al 2013) is not immediately apparent from this two-population model, but an extension of this model may be able to incorporate such techniques. Investigation into these types of spatial indicators is particularly important since critical slowing down in time is not always a reliable statistical indicator at coarse spatial widths (Boulton et al 2013).

Finally, a novel result of this paper is that directionality of parameter management to avoid critical transitions can make the difference between a successful recovery from the brink of extinction and a catastrophic mistake. In the two-population model, we showed that if the system is in the high/low state of Regime III in Figure 5, the transition to Regime II results in either a collapse of both populations (0/0 state) or a full recovery to the high/high stable state, depending on whether the parameter change crosses the left or right side of the cusp, respectively. This may be an essential feature of spatially-connected populations with variable Allee effects, and analysis of these dynamics should be incorporated into management strategies for ecological systems of a similar type. Similarly, these findings also point to ways to eradicate unwanted alien or invasive species, in the vein of (Liebhold and Bascompte 2003).

Allowing for heterogeneity in the growth rates r_i and threshold/carrying-capacity average γ_i between the two populations could also lead to interesting dynamics, and the effects of these parameters should be investigated. Increasing either γ_i should increase the resilience

of the system by pulling the dynamics further away from extinction. Increasing either r_i should make the corresponding population less sensitive to the migration effects from the other by strengthening the growth rate relative to the migration rate. An asymmetric passive diffusion would also be uninteresting, as the skewed movement of individuals would only increase the resilience of the sink population and decrease that of the source, though nonlinear migration terms may lead to surprising results (Holt 1996).

Given both the complexity and novelty of the results as well as the ubiquity of Allee effects and the generality of the model, we believe that we have uncovered important ecological conclusions that are robust and should apply broadly. The two-population model introduced in this paper provides a solid foundation for further research to build upon.

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