A model for a spatially structured metapopulation accounting for within patch dynamics

Andrew G. Smith*, Ross McVinish, Philip K. Pollett

School of Mathematics and Physics, University of Queensland, St Lucia, 4072, Queensland

Abstract

We develop a stochastic metapopulation model that accounts for spatial structure as well as within patch dynamics. Using a deterministic approximation derived from a functional law of large numbers, we develop conditions for extinction and persistence of the metapopulation in terms of the birth, death and migration parameters. Interestingly, we observe the Allee effect in a metapopulation comprising two patches of greatly different sizes, despite there being decreasing patch specific per–capita birth rates. We show that the Allee effect is due to way the migration rates depend on the population density of the patches.

Keywords: extinction, Markov process, metapopulation, partially ordered flow, spatially structured

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1. Introduction

The field of metapopulation ecology concerns the study of populations with a specific spatial structure where the population is separated into geographically distinct patches or islands. There has been a high level of interest in the field since the late 60s [1, 2], and this has continued to the present (see [3, 4, 5, 6] and references therein). Of significant concern to ecologists is the survival of the population and under what conditions the population might become extinct. Mathematical models have proved useful in addressing these questions.

*Corresponding author
Email address:* a.smith23@uq.edu.au (Andrew G. Smith)

Many models employ the presence–absence assumption, that is, they simply record whether or not each patch is occupied. This assumption is employed in the two most widely used metapopulation models: Levins' model [1] and Hanski's incidence function model [4]. Hanski's model has proven extremely successful in incorporating landscape structure and quality into the metapopulation dynamics. More generally, the presence–absence assumption has simplified modelling, data collection and analysis for a number of metapopulations [7, 8, 9, 10, 11, 12, 13, 14]. However, this assumption is not always adequate, for example in stock dynamics where more detail is required [15].

On the other hand, structured metapopulation models (SMMs) such as [16, 17, 18, 19, 20] model the births, deaths and migration of individuals directly, and the number of individuals present on each patch is recorded. The parameters of SMMs are easily interpreted as per–capita birth, death and migration rates, rather than abstract parameters such as patch level extinction and colonisation rates. Furthermore, SMMs give far more detail about the state of the metapopulation than is possible under the presence–absence assumption. Unfortunately, the SMMs cited above impose a number of unrealistic assumptions on the metapopulation; they fail to account for the spatial configuration of patches and assume that migration patterns are homogeneous across all patches.

We introduce a metapopulation model that is structured in respect of both spatial configuration and within patch dynamics. Our model has the form of a Markov population process introduced in [21]. Previous analyses of this class of models have focussed on determining expressions for moments and stationary distributions [3]. However, the restrictions that these analyses require are not natural in the present context since our model has an absorbing state corresponding to extinction. In this case, the stationary distribution would necessarily assign all its probability mass to the extinction state, and thus would not provide useful information about any quasi-stationary regime (being a common feature of metapopulation models [22]). Instead, we analyse this model by determining a simpler approximating differential equation based on the work of Kurtz [23] and Pollett [24].

Using the differential equation, we are able to determine conditions under which the

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metapopulation will go extinct quickly or persist for an extended period of time. We are also able to identify more complex dynamics such as the presence of an Allee effect for some range of parameters. An Allee effect refers to populations exhibiting an increasing per capita growth rate at low population density levels. When the per-capita growth rate is initially negative, a critical threshold emerges below which the population goes extinct. In populations displaying an Allee effect, conservation strategies need to be adapted to account for this, particularly if a critical threshold is present [25, section 5.1.4].

The paper is organized as follows. We begin, in Section 2, by detailing our model. The differential equation approximation is described in Section 3. In Section 4, we analyse the long–term behaviour of the approximating deterministic model, deriving conditions for extinction or persistence, and demonstrate the possibility of an Allee effect. Some examples are given to illustrate our results. Our conclusions are summarised in Section 5.

2. The Model

Our model is an example of Kingman's [21] Markov population process. Define, for any positive integer J, $\mathcal{S}^J$ as the set of J-vectors $n = (n_1, \ldots, n_J)$ where the n_i are non-negative integers. A simple Markov population process is a Markov process on a subset S of $\mathcal{S}^J$ whose only nonzero transitions rates are given by

$$q(n, n + e_i) = \alpha_i(n_i), \tag{1}$$

$$q(n, n - e_i) = \beta_i(n_i), \tag{2}$$

$$q(n, n - e_i + e_j) = \gamma_{ij}(n_i, n_j) \text{ for all } j \neq i, \tag{3}$$

where e_i is the unit vector with a 1 in the ith position and $q(x, y)$ is rate from state x to state y. In the present context, J is the number of patches in the metapopulation and $n_i(t)$ is the number of individuals occupying patch i at time t. The Markov process $(n(t), \ t \geq 0)$ describing the state of the metapopulation takes values in $S_N = \{0, \ldots, N_1\} \times \cdots \times \{0, \ldots, N_J\}$
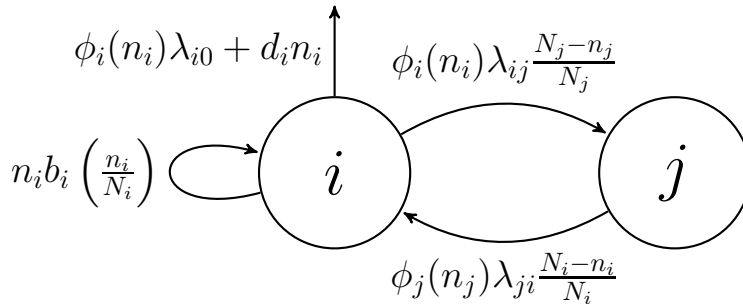
Figure 1: Illustration of the dynamics for patch i and migration to and from patch j.

and has nonzero transition rates

$$\alpha_i(n_i) = n_i b_i \left(\frac{n_i}{N_i} \right), \tag{4}$$

$$\beta_i(n_i) = \phi_i(n_i)\lambda_{i0} + d_i n_i, \tag{5}$$

$$\gamma_{ij}(n_i, n_j) = \phi_i(n_i)\lambda_{ij} \frac{N_j - n_j}{N_j} \quad \text{for all } j \neq i, \tag{6}$$

where $\phi_i(0) = 0$, $\phi_i(n) > 0$ for $n \geq 1$ and $b_i : [0,1] \mapsto \mathbb{R}_+$ such that $b_i(x) = 0$ for all $x \geq 1$. These rates correspond to: an increase on patch i due to a birth (4), a decrease on patch i due to a death or removal from the system (5) and a migration from patch i to patch j (6). The parameters d_i, λ_{ij} and N_i are the per–capita death rate, proportion of individuals migrating from patch i to patch j (or out of the system if $j = 0$) and the population ceiling for patch i, respectively. The birth rate function $b_i(\cdot)$ determines the per–capita birth rate given how densely populated patch i is. The function $\phi_i(\cdot)$, henceforth referred to as the *migration function*, represents the rate at which individuals leave patch i. Figure 1 illustrates these transitions.

We note that the models of Renshaw [3] and Arrigoni [17] have a number of features in common with our model. The main difference with Renshaw's model is in the linearity of the birth and migration rates. That linearity excludes the possibility of a carrying capacity at each patch. Arrigoni's model included catastrophes, that is, the possibility of the instantaneous death of all individuals on a given patch. However, it assumed that the birth, death and migration rates were the same for all patches and, as in Renshaw's model, it could not

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incorporate a carrying capacity at each patch.

3. Differential equation approximation

We will apply Theorem 3.1 of Pollett [24] which allows us to approximate the path of our process by the solution to a system of differential equations. To do this we first need to establish that our model is density dependent in the sense of Kurtz [23], or at least asymptotically density dependent [24].

Define the population ceiling as the sum of all patch ceilings $N := \sum_j N_j$. The population density at patch i is the number in patch i measured relative to N and is given by $X_i^{(N)}(t) := n_i(t)/N$. We are interested in the convergence of the density process $X_N := (X_1^{(N)}, \ldots X_J^{(N)})$ as $N \to \infty$. Define the relative ceiling for patch i as $M_i^{(N)} := N_i/N$ and assume that $M_i^{(N)} \to M_i > 0$ as $N \to \infty$. The density process X_N is a Markov process on the state space $E_N := S_N/N$.

Suppose that the functions $\hat{\phi}_i^{(N)} : [0, M_i^{(N)}] \to \mathbb{R}_+$ satisfy

$$\hat{\phi}_i^{(N)}\left(\frac{n}{N}\right) = \frac{\phi_i(n)}{N},$$

for all $n \geq 1$ and $N \geq 1$. Then, the rates (4), (5) and (6) can be written as

$$q(n, n+l) = N f_N\left(\frac{n}{N}, l\right),$$

where

$$f_N(x, l) = \begin{cases} x_i b_i\left(\frac{x_i}{M_i^{(N)}}\right) & \text{if } l = e_i, \\ \hat{\phi}_i^{(N)}(x_i)\lambda_{i0} + d_i x_i & \text{if } l = -e_i, \\ \hat{\phi}_i^{(N)}(x_i)\lambda_{ij}\left(1 - \frac{x_j}{M_j^{(N)}}\right) & \text{if } l = -e_i + e_j, \\ 0 & \text{otherwise.} \end{cases}$$

Let $F^{(N)}(x) := \sum_l l f_N(x, l)$ and observe that

$$F_i^{(N)}(x) = \left(b_i\left(\frac{x_i}{M_i^{(N)}}\right) - d_i\right) x_i$$

$$+ \sum_{j \neq i} \hat{\phi}_j^{(N)}(x_j)\lambda_{ji}\left(1 - \frac{x_i}{M_i^{(N)}}\right) - \hat{\phi}_i^{(N)}(x_i)\left(\lambda_{i0} + \sum_{j \neq i} \lambda_{ij}\left(1 - \frac{x_j}{M_j^{(N)}}\right)\right).$$

Define $E := [0, M_1] \times \ldots \times [0, M_J]$. Assume there exists bounded Lipschitz continuous functions $\hat{\phi}_i : [0, M_i] \to \mathbb{R}_+$ satisfying

$$\lim_{N \to \infty} \sup_{x \in [0, M_i]} \left| \hat{\phi}_i^{(N)}(x) - \hat{\phi}_i(x) \right| = 0, \quad \text{for all } i, \tag{7}$$

and also

$$\lim_{N \to \infty} \sup_{x \in [0, M_i]} \left| b_i \left(\frac{x_i}{M_i^{(N)}} \right) - b_i \left(\frac{x_i}{M_i} \right) \right| = 0. \tag{8}$$

We may then conclude that $F^{(N)}(x) \to F(x)$ as $N \to \infty$, *uniformly* on E, where

$$F_i(x) = \left(b_i \left(\frac{x_i}{M_i} \right) - d_i \right) x_i$$
$$+ \sum_{j \neq i} \hat{\phi}_j(x_j) \lambda_{ji} \left(1 - \frac{x_i}{M_i} \right) - \hat{\phi}_i(x_i) \left(\lambda_{i0} + \sum_{j \neq i} \lambda_{ij} \left(1 - \frac{x_j}{M_j} \right) \right),$$

for $i = 1, \ldots, J$. Therefore, the family of processes indexed by the population ceiling N is asymptotically density dependent according to Definition 3.1 of [24]. Next we apply Theorem 3.1 of [24], the analogue of Theorem 3.1 of Kurtz [23] for asymptotically density dependent families of processes. The conditions of this theorem are fulfilled as $f_N(x, l)$ is bounded on E for all N and l and is nonzero for only finitely many l. Recall that λ_{ij} is the proportion of individuals emanating from patch i who are destined for patch j. Thus,

$$\sum_{j \neq i} \lambda_{ij} + \lambda_{i0} = 1, \tag{9}$$

and so we may rewrite $F(x)$ as

$$F_i(x) = \left(b_i \left(\frac{x_i}{M_i} \right) - d_i \right) x_i - \hat{\phi}_i(x_i)$$
$$+ \sum_{j \neq i} \left(\hat{\phi}_j(x_j) \lambda_{ji} + \left(\hat{\phi}_i(x_i) \lambda_{ij} \frac{x_j}{M_j} - \hat{\phi}_j(x_j) \lambda_{ji} \frac{x_i}{M_i} \right) \right),$$

$i = 1, \ldots, J$. It can be seen that F is Lipschitz continuous on E. Hence, the conditions of Theorem 3.1 of [24] are satisfied, and we conclude that the density process converges in probability over finite time intervals to the solution $x(t, x_0)$ of the deterministic model

$$\frac{dx(t, x_0)}{dt} = F(x(t, x_0)), \quad x(0, x_0) = x_0, \tag{10}$$

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as N increases. More precisely, we have the following result.

Theorem 3.1. *Let $x(t, x_0)$ be the solution to (10). Suppose there exists bounded Lipschitz continuous functions $\hat{\phi}_i : [0, M_i] \to \mathbb{R}_+$ satisfying (7) and assume also that the functions b_i satisfy (8). If $X_N(0) \to x_0 \in E \backslash \partial E$ as $N \to \infty$ and $x(s, x_0) \in E \backslash \partial E$ for $0 \leq s \leq t$. Then, for every $t > 0$ and $\delta > 0$,*

$$\lim_{N \to \infty} \Pr \left(\sup_{s \leq t} |X_N(s) - x(s, x_0)| > \delta \right) = 0.$$

Although the above result holds only in the limit as $N \to \infty$, explicit bounds on $\Pr \left(\sup_{s \leq t} |X_N(s) - x(s, x_0)| > \delta \right)$ for finite N could be determined using Theorems 4.1 and 4.2 of [26]. Furthermore, the fluctuations of the stochastic process X_N about the deterministic trajectory $x(\cdot, x_0)$ can be scaled as $N \to \infty$ to yield a Gaussian diffusion in the limit. As the diffusion limit is not of immediate use in our analysis, we defer its description to the Appendix. These results go some way to justifying the use of the deterministic model (10) to approximate the behaviour of our metapopulation model when the population ceiling N is large. Note that, for a given population ceiling N, we expect the deterministic model to provide a better approximation to the stochastic model when the number of patches is small. In the extreme case where the number of patches is comparable to N, only a small number of individuals would occupy any given patch, a situation where a differential equation approximation would be ineffective.

In what follows, we identify the fixed points of our deterministic model, investigate their stability, and thus elucidate conditions for persistence and extinction of the metapopulation.

4. Equilibrium Behaviour

The basic problem we seek to address is to understand what happens to the metapopulation in the long term. If the population ceiling N is finite then it is known that the metapopulation will eventually go extinct. However, for N sufficiently large, the time to extinction may be very large and the metapopulation may settle into some quasi–equilibrium state before going extinct. In this section, we examine the quasi–equilibrium state of the

metapopulation described by the Markov population process (4) by examining the fixed points of the limiting deterministic model given by (10). We make the following assumptions about the population dynamics:

(A) The migration functions are linear: $\phi_i(n) = \phi_i n$, where $\phi_i > 0$ for all i (implying that $\hat{\phi}_i(x) = \phi_i x$ for all i).

(B) For all i and j, $\lambda_{ij} = 0$ implies $\lambda_{ji} = 0$.

(C) For all i and j, there is a finite sequence (a_k) such that $\lambda_{ia_1}\lambda_{a_1a_2}\ldots\lambda_{a_mj} \neq 0$.

(D) For all i, $b_i(x)$ is a continuously differentiable, strictly decreasing function on $[0,1]$ such that $b_i(x) = 0$ for all $x \geq 1$ and $xb_i(x)$ is strictly concave on $[0,1]$.

(E) The parameters ϕ_i, λ_{ij} and M_i satisfy $\phi_i\lambda_{ij}M_i = \phi_j\lambda_{ji}M_j$ for all i,j.

Assumption (A) stipulates that the rate at which individuals leave a patch is proportional to the number of individuals in that patch; as the patch becomes more crowded, individuals leave at a greater rate. Whilst it is true that this assumption simplifies our analysis, there is considerable empirical evidence to support density-dependent migration [27, 20], a linear migration term often being used [16, 17, 28]. Assumption (B) implies that all migration paths must allow two–way movement; if an individual moves from patch i to patch j, it must be possible to return without needing to go through other patches. Assumption (C) excludes the possibility that any patch or group of patches is isolated. If Assumption (C) did not hold, then the metapopulation could be divided into a number of smaller metapopulations that could each be analysed separately. Assumption (D) implies that as a patch becomes full and less space is available for new individuals, the birth rate decreases. When the patch is full, the birth rate is 0. In a empty network, Assumption (E) translates to every patch having the same maximum migration rate to any other patch. For example, in a symmetric case, $\lambda_{ij} = \lambda_{ji}$ for all i,j, individuals would migrate away faster from a smaller patch than a larger patch. Although this restriction is quite strict, it is not required for all of our results. Under these assumptions, we will analyse the behaviour of a population governed by (10).

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In our analysis, we employ the concept of a partially ordered flow. For vectors $a, b \in \mathbb{R}^J$, the inequality $a \leq b$ will mean that $a_i \leq b_i$ for all i while $a < b$ will mean $a \leq b$ with $a_j < b_j$ for at least one j. The solution $x(t, x_0)$ of the ODE (10) with initial condition $x(0) = x_0$, as a function of t and of x_0, is called the *flow* of F. Let $U \subset \mathbb{R}^J$ be a convex open set. The flow is then *partially ordered* on U if for any $a, b \in U$, $x(t, a) \leq x(t, b)$ for all $t \geq 0$ whenever $a \leq b$. According to Lemma 2.1 of [29], any flow F on a set $U \subset \mathbb{R}^n$ is partially ordered if all off–diagonal elements of $\nabla F(x)$ are nonnegative for all $x \in U$, that is, if $\nabla F(x)$ is a Metzler matrix. For our ODE (10) the off–diagonal elements of $\nabla F(x)$ are given by

$$\nabla F_{ij}(x) = \hat{\phi}'_j(x_j) \lambda_{ji} \left(1 - \frac{x_i}{M_i} \right) + \hat{\phi}_i(x_i) \frac{\lambda_{ij}}{M_j}.$$

Define the open set $U_\epsilon = (-\epsilon, M_1 + \epsilon) \times (-\epsilon, M_J + \epsilon)$ for some $\epsilon > 0$. Under Assumptions (A) and (B), $\nabla F_{ij}(x) \geq 0$ for ϵ sufficiently small. Thus, the flow of F is partially ordered on U_ϵ.

Proposition 4.1. *Assume (A) and (B) hold. The set $E := [0, M_1] \times \ldots \times [0, M_J]$ is a positive invariant set for the flow defined by (10). That is, if $x_0 \in E$, then $x(t, x_0) \in E$ for all $t \geq 0$.*

Proof. Note that $E \subset U_\epsilon$ and for any $x_0 \in E$, $\mathbf{0} \leq x_0 \leq M$. As the flow is partially ordered on U_ϵ, if $x_0 \in E$, then

$$x(t, \mathbf{0}) \leq x(t, x_0) \leq x(t, M), \quad t \geq 0. \tag{11}$$

Therefore, to show that E is a positive invariant set it is sufficient to show that $x(t, \mathbf{0}) \in E$ and $x(t, M) \in E$ for all $t \geq 0$. Consider the trajectory starting at M. The elements of $F(M)$ are given by

$$F_i(M) = - \left(d_i M_i + \hat{\phi}_i(M_i) \left(1 - \sum_{j \neq i} \lambda_{ij} \right) \right) = - \left(d_i M_i + \hat{\phi}_i(M_i) \lambda_{i0} \right) < 0.$$

Therefore, for all $s > 0$ sufficiently small, $x(s, M) < M$, which implies that $x(ns, M) \leq M$, where $n \in \mathbb{Z}_+$, again by partial ordering. Therefore, for all $t \geq 0$,

$$x(t, M) \leq M. \tag{12}$$

At the lower boundary, $F(\mathbf{0}) = \mathbf{0}$ so $x(t, \mathbf{0}) = \mathbf{0}$ for all $t \geq 0$. This, combined with (11) and (12), implies that $x(t, M) \in E$ for all $t \geq 0$. This completes the proof. $\square$

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4.1. Extinction

As noted earlier, although the eventual extinction of the Markov population process is certain, the process may take a very long time to reach the extinction state. However, if the deterministic process (10) converges to the extinction state quickly, then, from Theorem 3.1, it would be reasonable to conclude that the Markov population process also goes extinct quickly. The following theorem describes the behaviour of the deterministic process in a neighbourhood of the extinction state.

Theorem 4.1. *Assume (A) - (D) hold. If there exists a $y \in \mathbb{R}_+^J \backslash \{\mathbf{0}\}$ such that*

$$(b_i(0) - d_i - \phi_i)\, y_i + \phi_i \sum_{j \neq i}^J \lambda_{ij} y_j \leq 0, \quad \text{for all } i, \tag{13}$$

with strict inequality for at least one i, the fixed point $\mathbf{0}$ is asymptotically stable. If there is no $y \in \mathbb{R}_+^J \backslash \{\mathbf{0}\}$ satisfying (13), then $\mathbf{0}$ is unstable.

Proof. Under Assumption (A), $\mathbf{0}$ is a fixed point of (10), that is $F_i(\mathbf{0}) = 0$. The elements of the Jacobian of F at $\mathbf{0}$ are given by

$$\nabla F(\mathbf{0})_{ij} = \begin{cases} b_i(0) - d_i - \phi_i & \text{if } j = i \\[2mm] \phi_j \lambda_{ji} & \text{if } j \neq i. \end{cases}$$

As all parameters are non-negative, $J_0 := \nabla F(\mathbf{0})$ is a Metzler matrix. From Assumption (C), J_0 is irreducible, meaning for every pair (i, j) there is an integer m such that $(J_0^m)_{ij} > 0$. Henceforth we will exploit properties of J_0^T, noting that its eigenvalues are the same as those of J_0. Since J_0^T is also a Metzler matrix, Theorem 2.6(c) of [30] implies that J_0^T has a real eigenvalue r which is greater than the real part of any other eigenvalue of J_0^T. Furthermore, from Part (e) of that theorem, $r \leq 0$ if and only if there is a vector $y > \mathbf{0}$ such that $J_0^T y \leq \mathbf{0}$ and $r < 0$ if and only if $J_0^T y < \mathbf{0}$. The condition $J_0^T y \leq \mathbf{0}$ gives rise to (13). Now write $F(x)$ in (10) as

$$F(x) = J_0 x + \tilde{F}(x), \tag{14a}$$

where

$$\tilde{F}_i(x) = x_i \left(b_i \left(\frac{x_i}{M_i} \right) - b_i(0) \right) + \sum_{j \neq i} x_i x_j \left(\frac{\phi_i \lambda_{ij}}{M_j} - \frac{\phi_j \lambda_{ji}}{M_i} \right). \tag{14b}$$

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It can be seen that $\tilde{F}(x)$ is Lipschitz continuous on E and that

$$\lim_{||x|| \to 0} \frac{||\tilde{F}(x)||}{||x||} = 0. \tag{15}$$

If $r < 0$, then $\mathbf{0}$ is an asymptotically stable fixed point by Theorem 7.1 of [31]. If $r > 0$, then $\mathbf{0}$ is unstable by Theorem 7.3 of [31]. □

It must be noted that Theorem 4.1 does not deal with the case of equality in (13) for all i. This corresponds to the case of where the maximum eigenvalue of J_0 is 0. Our numerical studies have shown that, in such cases, the stability of $\mathbf{0}$ is model specific. This is demonstrated in Figure 2. In plot A, the trajectory begins with both patches being full and the metapopulation tends towards the extinction state. As the system is partially ordered, every other trajectory in E will also tend towards the extinction state implying it is globally stable. However, in plot B, the trajectory begins with both patches near extinction and the metapopulation moves away to a nonzero fixed point. Hence, in the second case, the extinction state is unstable.

The conditions given in Theorem 4.1 are not easily interpreted, particularly for metapopulations consisting of a large number of patches. The following corollaries provide simpler sufficient conditions for stability/instability of the extinction state.

Corollary 4.1. *Assume (A) - (D) hold. If*

$$\frac{b_i(0)}{d_i + \phi_i \lambda_{i0}} \leq 1, \quad \text{for all } i, \tag{16a}$$

with a strict inequality for at least one i, $\mathbf{0}$ is asymptotically stable, while if

$$\frac{b_i(0)}{d_i + \phi_i \lambda_{i0}} > 1, \quad \text{for all } i, \tag{16b}$$

$\mathbf{0}$ *is unstable.*

Proof. Take $y = \mathbf{1}$. The condition for the asymptotic stability of $\mathbf{0}$ from Theorem 4.1 is satisfied if

$$b_i(0) - d_i - \phi_i + \phi_i \sum_{j \neq i} \lambda_{ij} \leq 0, \quad \text{for all } i, \tag{17}$$
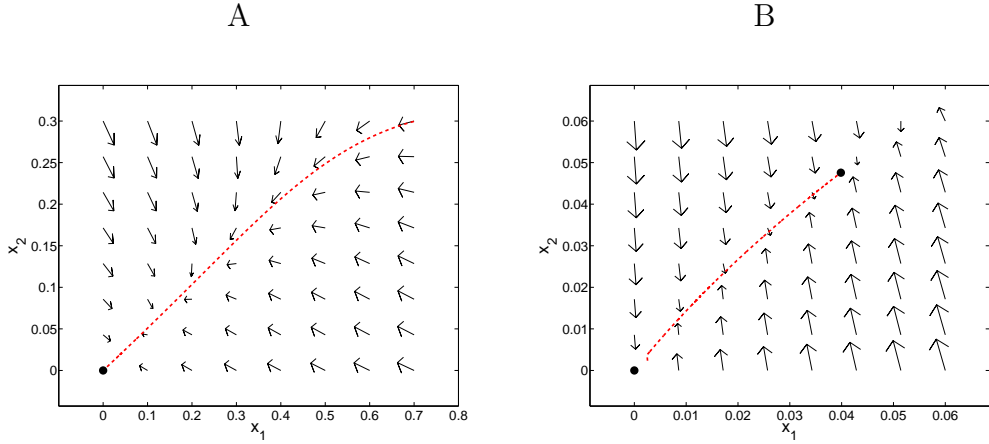
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Figure 2: Illustrating the different behaviour ODE (10) exhibits when $r = 0$ for a $J = 2$ system. The red dotted lines are the trajectories for a given initial condition and the black dots are fixed points. The birth rate function used was $b_i(x/M_i) = b_i(0)(1 - x/M_i)$. The parameters used were A $b_1(0) = 0.1$, $b_2(0) = 0.5$, $d_1 = 0.2$, $d_2 = 0.1$, $\phi_1 = 0.2$, $\phi_2 = 0.6$, $M_1 = 0.7$ and $M_2 = 0.3$, whilst $\lambda_{10} = 0.5$ and $\lambda_{20} = 0$ and B $b_1(0) = 1.3$, $b_2(0) = 0.54$, $d_1 = 0.6$, $d_2 = 0.38$, $\phi_1 = 0.75$, $\phi_2 = 0.64$, $M_1 = 0.63$ and $M_2 = 0.37$, while $\lambda_{10} = 0$, and $\lambda_{20} = 0.95$.

with a strict inequality for at least one i. Using (9) we may express (17) as $b_i(0) - d_i - \phi_i \lambda_{i0} \leq 0$, for all i, which gives rise to (16a). To prove the second part of the corollary, we can apply Corollary 1 of Theorem 2.8 of [30] to J_0 to give the following lower bound on r, the largest real part of the eigenvalues of J_0:

$$\min_i \left(b_i(0) - d_i - \phi_i + \sum_{j \neq i} \phi_i \lambda_{ij} \right) \leq r. \tag{18}$$

Recalling (9) again, (18) becomes

$$\min_i \left(b_i(0) - d_i - \phi_i \lambda_{i0} \right) \leq r.$$

If (16b) holds, then $\min_i \left(b_i(0) - d_i - \phi_i \lambda_{i0} \right) > 0$ and $r > 0$. Hence, **0** is unstable from Theorem 4.1. $\qquad \square$

Remark: For homogeneous systems, where $b_i(0)/(d_i + \phi_i \lambda_{i0}) = \alpha \neq 1$ for all i, conditions (16) are almost necessary and sufficient for the stability of **0**. When $\alpha = 1$, the maximum

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eigenvalue of J_0 is 0 and the stability of $\mathbf{0}$ is not characterised by determining the maximum eigenvalue of J_0, as stated previously.

Corollary 4.2. *Assume (A) - (D) hold. Then if*

$$\frac{b_i(0)}{d_i + \phi_i} > 1, \quad \text{for at least one } i, \tag{19}$$

$\mathbf{0}$ *is unstable.*

Proof. If (19) holds for some i, then, for any vector $y \in \mathbb{R}^J_+\backslash\{\mathbf{0}\}$,

$$y_i\left(b_i(0) - d_i - \phi_i\right) + \phi_i \sum_{j \neq i} y_j \lambda_{ij} > 0.$$

Thus there is no $y \in \mathbb{R}^J_+\backslash\{\mathbf{0}\}$ satisfying inequality (13) and, according to Theorem 4.1, $\mathbf{0}$ is unstable. $\qquad\square$

The above results only address the behaviour of the system when it starts in a neighbourhood of the extinction state. It may be that the metapopulation can persist if it is initially densely populated, such as for a metapopulation with Allee effect [32, 25]. Due to the partial ordering of the flow, an Allee effect would be observed if there exists a nonzero fixed point and $\mathbf{0}$ were asymptotically stable. The following result shows that if Assumption (E) is imposed and inequality (13) holds, then the metapopulation goes extinct regardless of the initial condition. Hence, the metapopulation does not display an Allee effect under Assumption (E).

Theorem 4.2. *Assume (A) - (E) hold. If there exists a $y \in \mathbb{R}^J_+\backslash\{\mathbf{0}\}$ such that (13) holds, then $x(t, x_0) \to \mathbf{0}$ for all $x_0 \in E$.*

Before giving the proof of this theorem we first derive an upper bound on $x(t, x_0)$.

Lemma 4.1. *Assume (A) - (E) hold and define $y(t, y_0)$ as the solution to*

$$\frac{dy}{dt} = J_0 y, \quad y(0) = y_0. \tag{20}$$

Then $x(t, x_0) \leq y(t, x_0)$ for all $t \geq 0$.

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Proof. The solution to (20) is given by $y(t, x_0) = e^{J_0 t} x_0$ and we can write the unique solution to (10) as

$$x(t, x_0) = y(t, x_0) + \int_0^t e^{(t-s)J_0} \tilde{F}(x(s)) ds, \tag{21}$$

where $\tilde{F}(x)$ is given by (14b). Under Assumptions (D) and (E), $\tilde{F}_i(x) \leq 0$ for all $x \in E$. Furthermore, as J_0 is an irreducible Metzler matrix (from the proof of Theorem 4.1), we can apply Theorem 2.7 of [30] to conclude that e^{tJ_0} is positive for all $t \geq 0$. It follows that $x(t, x_0) \leq y(t, x_0)$ for all $t \geq 0$. □

We can now use Lemma 4.1 to show that **0** is globally stable under the conditions of Theorem 4.2.

Proof of Theorem 4.2. When there exists $y \in \mathbb{R}_+^J \backslash \{\mathbf{0}\}$ such that (13) holds, the eigenvalue of J_0 with largest real part, r, satisfies $r \leq 0$ and has algebraic multiplicity one [30, Theorem 2.6 (a,c,d,e)]. Applying Theorem 6.1(b) of [31], there exists a positive constant C such that $\|y(t, x_0)\| \leq C\|x_0\|$. Therefore, $y(t, x_0)$ is bounded uniformly in $t \geq 0$ and $x_0 \in E$. Next we know $x_0 \leq M$ for all $x_0 \in E$. Therefore, if $x(t, M) \to \mathbf{0}$ then, due to partial ordering, $x(t, x_0) \to \mathbf{0}$ for all $x_0 \in E$ also. So we will only consider $x(t, M)$. As E is a positive invariant set, from Proposition 4.1, $x(s, M) \leq M$ for any $s \geq 0$. Due then to partial ordering $x(t, x(s, M)) = x(s + t, M) \leq x(s, M) \leq M$ for any $s, t \geq 0$. Hence, $x(t, M)$ is monotone decreasing and bounded, implying that it has a limit as $t \to \infty$ which we denote by α. The proof will be complete if we can show that $\alpha = \mathbf{0}$.

Suppose $r < 0$. From Theorem 4.5 of [33], $y(t, x_0) \to \mathbf{0}$ for any $x_0 \in E$. Since $y(t, x_0)$ bounds $x(t, x_0)$, $x(t, x_0) \to \mathbf{0}$ for any $x_0 \in E$, showing $\alpha = \mathbf{0}$. Now suppose $r = 0$ and that $\mathbf{0} < \alpha$. With Assumptions (D) and (E), this implies that there exists a $\beta > \mathbf{0}$ such that $-\tilde{F}(x(t, M)) \geq \beta$ for all $t > 0$. Since e^{tJ_0} is positive for all $t \geq 0$ [30, Theorem 2.7], it follows that

$$\int_0^t e^{(t-s)J_0} \tilde{F}(x(s, M)) ds \leq -\int_0^t e^{(t-s)J_0} \beta ds. \tag{22}$$

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From Theorem 2.7 of [30] we know that $e^{sJ_0} = wv^T + O(e^{\lambda s})$, elementwise, as $s \to \infty$, where $\lambda < 0$, and w and v are the positive right and left eigenvectors of J_0 corresponding to the eigenvalue r normed so that $v^T w = 1$. Therefore, the integral on the right-hand side of (22) tends to negative infinity as $t \to \infty$. Hence, from Lemma 4.1 (equation (21)) and recalling that y is bounded, we can take t sufficiently large so that $x(t, M) < \mathbf{0}$. This is a contradiction since, from Proposition 4.1, $x(t, M) \in E$ for all t. Therefore $\alpha = \mathbf{0}$ and $x(t, x_0) \to \mathbf{0}$ for all $x_0 \in E$. □

4.2. Persistence

Theorem 4.1 shows how the metapopulation behaves when near extinction but does not provide any information concerning the behaviour of the metapopulation away from the extinction state. Theorem 4.2 provides a complete description of the metapopulation when the model satisfies Assumption (E) and inequality (13). This subsection studies the behaviour of the metapopulation when condition (13) does not hold.

Theorem 4.3. *Assume (A) – (D) hold. If there is no $y \in \mathbb{R}_+^J \backslash \{\mathbf{0}\}$ satisfying (13), E contains at least one nonzero fixed point $x^{(1)*}$ and, for all x_0 such that $\mathbf{0} < x_0 \leq x^{(1)*}$, $x(t, x_0) \to x^{(1)*}$.*

Proof. Suppose that there is no $y \in \mathbb{R}_+^J \backslash \{\mathbf{0}\}$ satisfying (13), then the eigenvalue of J_0 with largest real part, r, satisfies $r > 0$ and has algebraic multiplicity one [30, Theorem 2.6 (a,c,d,e)]. The corresponding eigenvector v of J_0 satisfies $v > 0$. Finally, as E is a positive invariant set we may apply Theorem 2.8 of [29]. Combining parts (1), (4) and (5) of Theorem 2.8 [29], we can conclude that either $x(t, x_0) \to x^{(1)*}$ or $\|x(t, x_0)\| \to \infty$ for all $x_0 \geq \mathbf{0}, x_0 \neq \mathbf{0}$ where $x^{(1)*} > \mathbf{0}$. As E is a positive invariant set, $\|x(t, x_0)\| \leq \|M\|$. Hence, $x(t, x_0) \to x^{(1)*}$ for all x_0 such that $\mathbf{0} < x_0 \leq x^{(1)*}$. □

This theorem shows that for sufficiently small $x_0 \neq \mathbf{0}$, trajectories will tend to a nonzero fixed point. Furthermore, due to partial ordering, $x^{(1)*} \leq \liminf_{t \to \infty} x(t, x_0)$ for all $x_0 \in E \backslash \{\mathbf{0}\}$, implying that the metapopulation will persist. However, Theorem 4.3 does not pre-

clude the possibility of another nonzero fixed point. This issue is addressed in the following theorem under Assumption (E).

Theorem 4.4. *Assume (A) - (E) hold. If there is no $y \in \mathbb{R}_+^J \backslash \{\mathbf{0}\}$ satisfying (13), then there is a unique nonzero fixed point $x^{(1)*}$ and $x(t, x_0) \to x^{(1)*}$ for all $x_0 \in E \backslash \{\mathbf{0}\}$.*

As in the proof of Theorem 4.2, we first derive an upper bound on $x(t, x_0)$.

Lemma 4.2. *Assume (A) - (E) hold and let $y(t, y_0)$ be the solution to*

$$\frac{dy}{dt} = J_1(y - x^{(1)*}), \quad y(0) = y_0,$$

where $J_1 = \nabla F(x^{(1)*})$. Then $x(t, x_0) \leq y(t, x_0)$ for all $t \geq 0$.

Proof. We know that $y(t, x_0) = x^{(1)*} + e^{J_1 t}(x_0 - x^{(1)*})$. With the simple change of coordinates $z = x(t, x_0) - x^{(1)*}$, together with Assumption (E), we can write the solution to (10) as

$$x(t, x_0) = y(t, x_0) + \int_0^t e^{(t-s)J_1} \bar{F}(x(s, x_0))ds, \tag{23}$$

where $\bar{F}(x)$ is given by

$$\bar{F}_i(x) = x_i \left(b_i \left(\frac{x_i}{M_i} \right) - b_i \left(\frac{x_i^{(1)*}}{M_i} \right) \right) + \left(x_i^{(1)*} - x_i \right) b_i' \left(\frac{x_i^{(1)*}}{M_i} \right) \frac{x_i^{(1)*}}{M_i}.$$

Under Assumption (E), $\bar{F}(x(s, x_0)) \leq \mathbf{0}$ for $x(s, x_0) \in E$. As in Lemma 4.1, $e^{J_1 t}$ is a positive matrix since J_1 is an irreducible Metzler matrix. We then conclude that $x(t, x_0) \leq y(t, x_0)$ for all $t \geq 0$. $\qquad\square$

Proof of Theorem 4.4. From Theorem 4.3 it is known that for all x_0 such that $\mathbf{0} < x_0 \leq x^{(1)*}$, $x(t, x_0) \to x^{(1)*}$. If we can show that $x(t, M) \to x^{(1)*}$, then we can conclude that $x(t, x_0) \to x^{(1)*}$ for any $x_0 \in E \backslash \mathbf{0}$ as the flow is partially ordered. Following the arguments in the proof of Theorem 4.1, $\lim_{t \to \infty} x(t, M)$ exists. Denote this limit by α. The proof will be complete if we can show that $\alpha = x^{(1)*}$. As in Theorem 4.1, J_1 has a real eigenvalue r_1 which is greater than the real part of any other eigenvalue of J_1.

Suppose $r_1 < 0$. From Theorem 4.5 of [33], $y(t, x_0) \to x^{(1)*}$ for any $x_0 \in E$. Since $y(t, x_0)$ bounds $x(t, x_0)$, $x(t, x_0) \to x^{(1)*}$ for any $x_0 \in E$, showing $\alpha = x^{(1)*}$. Now suppose that

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$r_1 = 0$ and $x^{(1)*} < \alpha$. With Assumptions (D) and (E) this implies that there exists a $\beta > \mathbf{0}$ such that $-\bar{F}(x(t, M)) \geq \beta$ for all $t > 0$. Note that e^{tJ_1} is positive for all $t \geq 0$ as J_1 is a Metzler matrix [30, Theorem 2.7]. It now follows from Lemma 4.2 (equation (23)) and recalling that y is bounded, we can take t sufficiently large so that $x(t, M) < x^{(1)*}$. This is a contradiction as the flow is partially ordered and $x^{(1)*}$ is a fixed point. Therefore $\alpha = x^{(1)*}$ and $x(t, x_0) \to x^{(1)*}$ for all $x_0 \in E \backslash \mathbf{0}$. $\qquad \square$

As before, the conditions for persistence can be quite difficult to interpret. If we assume that Assumption (A) to (E) hold then, according to Theorem 4.4, if condition (13) does not hold, the population will tend towards a unique nonzero fixed point. We can write this fixed point explicitly if $b_i(0)/(d_i + \phi_i \lambda_{i0}) = \alpha > 1$ for all i. It is rather simple to show that $x^* \in E \backslash \{\mathbf{0}\}$, with elements $x_i^* = M_i(1 - \alpha^{-1})$, satisfies $F(x^*) = \mathbf{0}$. Furthermore, all trajectories converge to x^*.

4.3. Allee Effect

Under Assumption (E), we have shown that when there exists a $y \in \mathbb{R}_+^J \backslash \{\mathbf{0}\}$ satisfying (13), the metapopulation will tend towards the extinction state $\mathbf{0}$. Otherwise, the metapopulation will tend towards a nonzero unique equilibrium level regardless of its initial value. However, it has been observed for some populations that whether it progresses towards extinction or a nonzero equilibrium depends on the initial population size. This is known as the Allee effect [34]. Courchamp et al. [35] have shown the existence of an Allee effect for metapopulations in their study of the African Wild dog, *Lycaon pictus*.

We investigate the possibility of our metapopulation model displaying an Allee effect when Assumption (E) does not hold. To address this question, we focus on the two–patch metapopulation with the *decreasing* birth rate function $b_i(x/M_i) = b_i(0)(1 - x/M_i)$. To simplify our notation, below we will write b_i for $b_i(0)$. Let $M_1 = 1 - \varepsilon$ and $M_2 = \varepsilon$ and $y_i := x_i^*/M_i = y_i^{(0)} + \varepsilon y_i^{(1)} + \varepsilon^2 y_i^{(2)} + \ldots$ for $i = 1, 2$, where x_i^* satisfies $F(x^*) = 0$. Using perturbation theory, an expansion for the fixed points of the system is determined.

The fixed points are the solutions to a system of two quadratic equations in two variables, entailing four solutions. One of these is $\mathbf{0}$ and, for sufficiently small $\varepsilon > 0$, we can approximate

the remaining three solutions $\mathbf{y}_{(i)} := (y_1, y_2)$ to first order by

$$\mathbf{y}_{(1)} = \begin{pmatrix} \frac{\phi_2 \lambda_{21} C_1}{(d_1 + \phi_1 - b_1 - C_1 \phi_1 \lambda_{12})} \varepsilon + \mathrm{O}\left(\varepsilon^2\right) \\ C_1 + C_3(C_1)\varepsilon + \mathrm{O}\left(\varepsilon^2\right) \end{pmatrix} \tag{24a}$$

$$\mathbf{y}_{(2)} = \begin{pmatrix} \frac{\phi_2 \lambda_{21} C_2}{(d_1 + \phi_1 - b_1 - C_2 \phi_1 \lambda_{12})} \varepsilon + \mathrm{O}\left(\varepsilon^2\right) \\ C_2 + C_3(C_2)\varepsilon + \mathrm{O}\left(\varepsilon^2\right) \end{pmatrix} \tag{24b}$$

$$\mathbf{y}_{(3)} = \begin{pmatrix} 1 - \frac{\phi_1 \lambda_{10} + d_1}{b_1} - \frac{d_2 + \phi_2 \lambda_{20}}{b_1 - d_1 - \phi_1 \lambda_{10}} \varepsilon + \mathrm{O}\left(\varepsilon^2\right) \\ 1 - \frac{b_1(d_2 + \phi_2 \lambda_{20}) + \phi_2 \lambda_{21}(d_1 + \phi_1 \lambda_{10})}{\phi_1 \lambda_{12}(b_1 - d_1 - \phi_1 \lambda_{10})} \varepsilon + \mathrm{O}\left(\varepsilon^2\right) \end{pmatrix}, \tag{24c}$$

where

$$C_1 = \frac{1}{2}\left(1 + \alpha\left(R_1^{(1)^{-1}} - 1\right) - R_0^{(2)^{-1}} + \sqrt{\left(1 + \alpha\left(R_1^{(1)^{-1}} - 1\right) - R_0^{(2)^{-1}}\right)^2 + \gamma}\right),$$

$$C_2 = \frac{1}{2}\left(1 + \alpha\left(R_1^{(1)^{-1}} - 1\right) - R_0^{(2)^{-1}} - \sqrt{\left(1 + \alpha\left(R_1^{(1)^{-1}} - 1\right) - R_0^{(2)^{-1}}\right)^2 + \gamma}\right),$$

$$\gamma = \alpha\left(R_0^{(1)^{-1}} - 1\right)\left(R_1^{(2)^{-1}} - 1\right) + R_0^{(2)^{-1}} - 1, \tag{25}$$

and

$$\alpha = \frac{b_1}{\phi_1 \lambda_{12}}, \quad R_0^{(i)} = \frac{b_i}{d_i + \phi_i \lambda_{i0}}, \quad R_1^{(i)} = \frac{b_i}{d_i + \phi_i}, \quad i = 1, 2.$$

We do not give the expression for $C_3(x)$ here owing to its length.

For the metapopulation to display an Allee effect, $\mathbf{0}$ must be stable. Using Theorem 4.1, the fixed point $\mathbf{0}$ is stable if there exists $y \in \mathbb{R}_+^2 \backslash \{\mathbf{0}\}$ such that

$$y_1(b_1 - d_1 - \phi_1) + \phi_1 y_2 \lambda_{12} \leq 0, \tag{26}$$

$$y_2(b_2 - d_2 - \phi_2) + \phi_2 y_1 \lambda_{21} \leq 0, \tag{27}$$

with strict inequality in one of (26) and (27). Such a y exists if $d_i + \phi_i - b_i > 0$ for $i = 1, 2$ and

$$1 < \frac{(d_1 + \phi_1 - b_1)(d_2 + \phi_2 - b_2)}{\phi_1 \lambda_{12} \phi_2 \lambda_{21}}. \tag{28}$$

Inequality (28) implies $\gamma > 0$ which implies $C_1 > 0$. A nonzero fixed point is present in $[0, 1]^2$ if $C_1 < 1$, which is satisfied if

$$R_0^{(1)} > \alpha \frac{\left(1 + \frac{1}{3} R_1^{(2)^{-1}}\right)}{\left(R_0^{(2)^{-1}} - 1\right)}. \tag{29}$$
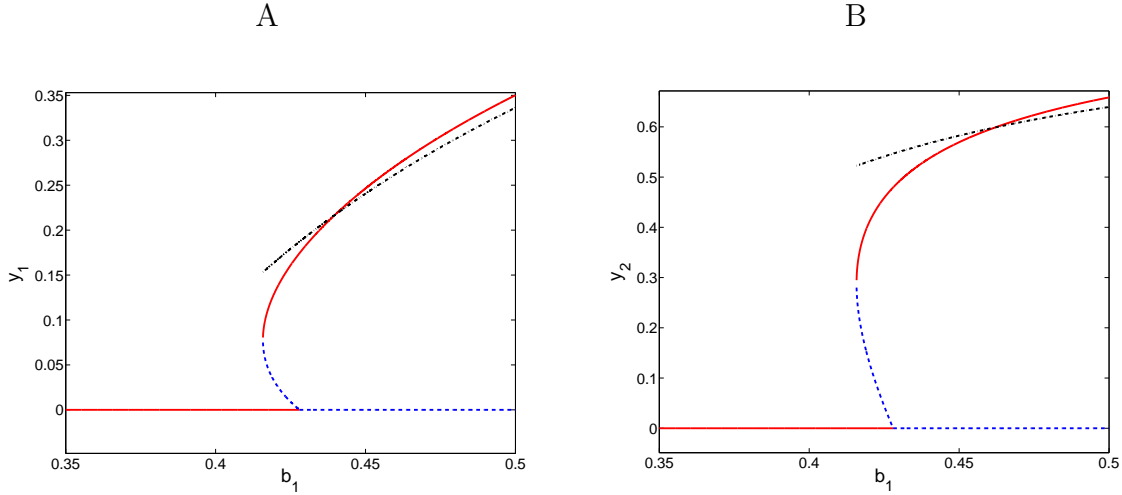
Figure 3: The red solid line represents stable fixed points, the blue dashed line represents unstable fixed points and the black dash-dot line represents the first order approximation (24c). Parameters used for plots A and B were $b_2 = 0.1$, $d_1 = 0.1$, $d_2 = 0.7$, $\phi_1 = 0.4$, $\phi_2 = 0.9$, $M_1 = 0.99$ and $M_2 = 0.01$, while $\lambda_{10} = 0.4$ and $\lambda_{20} = 0.5$.

Therefore, if the metapopulation parameters are such that $R_0^{(1)} > 1$, $\gamma > 0$ and (29) is met, then there exists an $\varepsilon > 0$ sufficiently small such that the three points $\mathbf{0}$, $\mathbf{y}_{(1)}$ and $\mathbf{y}_{(3)}$ are contained in $[0, 1]^2$.

Thus we have one stable fixed point at $\mathbf{0}$ and two nonzero fixed points whose stability is unknown. Let $x^{(i)*}$, $i = 1, 2$, denote the nonzero fixed points. As the flow is partially ordered, for any x_0 such that $x^{(i)*} \leq x_0$, we have $x^{(i)*} \leq \liminf_{t \to \infty} x(t, x_0)$. Therefore, the metapopulation will persist if it is initially sufficiently large. We can conclude that the metapopulation can display an Allee effect for a certain range of parameters. Figure 3 plots the scaled fixed points of a metapopulation as a function of b_1. The Allee effect is present when there is a dotted line, representing an unstable fixed point, between two solid lines, representing stable fixed points. In this example, the Allee effect is present when b_1 is between 0.415 and 0.428. This also illustrates the sensitivity of the metapopulation to disturbance, as only a very small change in the birth rate on the larger patch is needed to reduce the occupancy of the metapopulation from $(y_1, y_2) \approx (0.1, 0.3)$ to the extinction state.
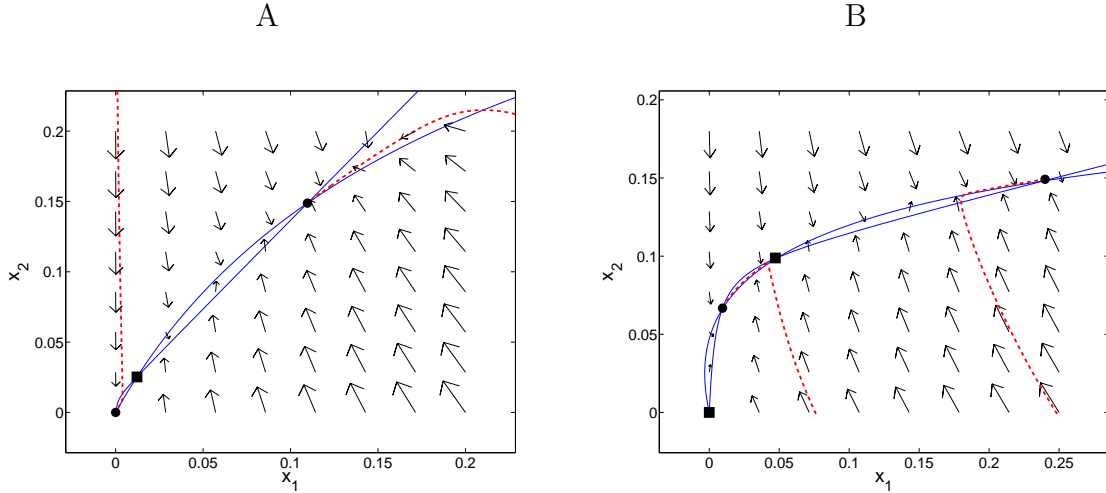
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Figure 4: The red dotted lines are the deterministic trajectories imposed by the flow (10), the squares are unstable fixed points, the dots are stable fixed points and the solid blue lines are the nullclines. Parameters used for plot A were $b_1 = 0.56$, $b_2 = 0.06$, $d_1 = 0.02$, $d_2 = 0.14$, $\phi_1 = 0.55$, $\phi_2 = 0.09$, $M_1 = 0.54$ and $M_2 = 0.46$, while $\lambda_{10} = 0.31$, and $\lambda_{20} = 0.99$. Parameters used for plot B were $b_1 = 5.24$, $b_2 = 7.5$, $d_1 = 1.14$, $d_2 = 5.59$, $\phi_1 = 7.03$, $\phi_2 = 0.29$, $M_1 = 0.78$ and $M_2 = 0.22$, while $\lambda_{10} = 0.06$ and $\lambda_{20} = 0.51$.

Although we have only demonstrated the Allee effect for a two–patch metapopulation where the patch ceilings are significantly different, numerical results show that the Allee effect can be present in metapopulations where the ceilings are not significantly different. Figure 4A shows a phase plane diagram for such a system and illustrates the different long term behaviour the system exhibits with different initial points. In one case the system starts with patch 1 full and patch 2 is empty, and the system converges to the largest fixed point. However, in the other case, patch 2 is full and patch 1 is empty, and the system goes extinct.

In Figures 3 and 4A, the three fixed points are partially ordered with the largest fixed point stable and the other nonzero fixed point unstable. There is some theoretical evidence that this holds in general. If all the eigenvalues of $\nabla F(x^{(2)*})$ have negative real parts, then Proposition 2.9 of [29] implies that $x^{(1)*} \leq x^{(2)*}$ and at least one eigenvalue of $\nabla F(x^{(1)*})$ has nonnegative real part. On the other hand, if one of the eigenvalues of $\nabla F(x^{(1)*})$ has

positive real part, then Theorem 2.8 of [29] implies that $x^{(1)*} \leq x^{(2)*}$ and all the eigenvalues of $\nabla F(x^{(2)*})$ have nonnegative real parts. Difficulties in dealing with the case where the eigenvalues of $\nabla F(x^{(i)*})$ have real parts equal to 0 prevent us from proving the general result.

Metapopulation models exhibiting an Allee effect are not new. Both Amarasekare [32] and Zhou & Wang [36] have proposed models displaying an Allee effect. However, in contrast to those models, the Allee effect observed here is not due to a manipulation of the birth rate function. Without migration between patches, our metapopulation model will not exhibit the Allee effect; it is induced by the migration of individuals as we now describe.

For a metapopulation to display an Allee effect, it is necessary that the extinction state be stable and for there to be a non-zero equilibrium. The non-zero equilibrium derived through perturbation analysis arises as follows. When the small patch is near capacity, migration between the two patches is reduced to a very low level. This has different effects on the two patches. The population dynamics on the large patch are dominated by the birth and death events. As the per-capita birth rate is initially larger than the death rate, a stable population becomes established. On the small patch, the immigration rate is still considerable relative to the size of the patch, and is sufficient to maintain the population close to capacity.

The extinction state can be seen to be stable by considering what happens when the populations on both patches are small relative to capacity. When the population on the small patch is far from capacity, the per-capita emigration rate on the large patch is significant. The birth rate is not sufficiently large to balance the deaths and emigration events resulting in a decreasing population on the large patch. As previously noted, the small patch has a high per-capita death rate. At the non-zero equilibrium, this was balanced by immigration from the large patch. However, when the metapopulation is near extinction, the migration from the large patch is much smaller and is no longer sufficient to balance the high death rate on the small patch.

We have so far focussed on the case where **0** is stable, that is, when the quantity γ given by equation (25) is greater than zero. However, interesting behaviour can also be observed if $\gamma <$

0. In that case, if $\left(1 + \alpha\left({R_1^{(1)}}^{-1} - 1\right) - {R_0^{(2)}}^{-1}\right)^2 > |\gamma|$ and $1 + \alpha\left({R_1^{(1)}}^{-1} - 1\right) - {R_0^{(2)}}^{-1} > 0$, there potentially exists an $\varepsilon > 0$ sufficiently small such that all four fixed points are in $[0, 1]^2$. With $\gamma < 0$, $\mathbf{0}$ is unstable, and hence trajectories tend away from $\mathbf{0}$ (the system persists regardless of the initial values). This possibility is discussed by Courchamp et al. [25, section 6.5.3], where Allee effects occur at intermediate population sizes or densities, resulting in up to three interior steady states, two of which are locally stable. This type of behaviour is illustrated in Figure 4B. One trajectory starting with patch 2 empty and patch 1 at 8% capacity tends towards a nonzero fixed point. However, when patch 1 begins at 32% capacity the trajectory tends to a larger (by partial ordering) fixed point. These two fixed points are also separated by a unstable fixed point.

4.4. Example

We now consider the metapopulation of sea otter (*Enhydra lutris*) in the north–east Pacific Ocean, which has been studied by various groups [39, 40]. Our purpose here is to illustrate the results obtained in the previous section, rather than provide a complete description of the population. Estes [40] studied five populations in this region: Attu Island, south–east Alaska, British Columbia, Washington State and central California. The migration rate between these 5 locations is not large. However, Amchitka Island, a previously unoccupied island adjacent to Attu Island, became occupied with sea otters. We consider a two–patch model to describe the evolution of the sea otter population in these two islands. Siniff and Ralls [39] determined an age distribution for the lifespan of the sea otter from which we can determine the average age of a female to be 5.18 years. Therefore, we set $d_i = 0.2 \approx 5.18^{-1}$ per year for both islands. Since the reproductive rate of females is between 0.43 and 0.45 per year [40], we set $b_i(x) = 0.44(1 - x/M_i)$. The per–capita migration rate ϕ_i is set to be the inverse of the average time an individual spends on island i before migrating. Finally, since Attu Island is approximately three times the size of Amchitka Island, we set $M_1 = 0.75$ (Attu) and $M_2 = 0.25$ (Amchitka).

From Corollary 4.2, if the average time an otter spends on one island before migrating is greater than 4.17 years, the extinction fixed point $\mathbf{0}$ is unstable and trajectories will tend

away from it. In that case, Theorem 4.3 implies the population will persist.

Next we consider the case where the average time an otter spends on one island before migrating is less than 4.17 years. By Theorem 4.1, extinction occurs if there exists a $y \in \mathbb{R}_+^2 \backslash \{\mathbf{0}\}$ such that inequalities (26) and (27) hold, equivalently, if inequality (28) holds. Rearranging inequality (28), we see that if the average time spent on one island is greater than $4.17(1 - \lambda_{12}\lambda_{21})$ years, the population will persist. However, if the average time spent on Attu Island and Amchitka Island before migrating are both less than $4.17(1 - \lambda_{12}\lambda_{21})$ years and

$$\phi_i^{-1} > \frac{4.17 \left[4.17\left(1 - \lambda_{12}\lambda_{21}\right) - \phi_j^{-1}\right]}{4.17 - \phi_j^{-1}}, \quad i, j \in \{1, 2\}, \; j \neq i, \tag{30}$$

then the population will persist. If none of these conditions is met, the population will become extinct. Note that if $4.17\left(1 - \lambda_{12}\lambda_{21}\right) < \phi_i^{-1} < 4.17$ for any i, (30) will automatically be satisfied.

These scenarios are illustrated in Figure 5. In plots A – C the average time spent on Attu Island is 10 years ($\phi_1 = 0.1$), while the average time spent on Amckitka Island is 1.25 years ($\phi_2 = 0.8$). The connectivity between patches is very weak, with $\lambda_{12} = 0.1$ and $\lambda_{21} = 0.05$. However, from Corollary 4.2, the metapopulation persists. In D – F, ϕ_1 is increased to 0.5, but $\lambda_{12} = 0.9$ and $\lambda_{21} = 0.4$. As inequality (30) is satisfied, the metapopulation persists. Finally, in G – I, ϕ_1 is increased to 0.7 years. Now, inequality (30) is not satisfied and the metapopulation goes extinct. With the chosen values for the birth and death rates, it is not possible for condition (29) to be satisfied, and so this system will not exhibit the Allee effect.

5. Discussion and Conclusion

We have proposed a structured metapopulation model that incorporates heterogeneous within patch dynamics and spatial structure, and identified conditions under which the metapopulation persists or goes extinct. As the extinction state is absorbing, we are not able to identify these conditions by identifying a stationary distribution for the model. Instead, we have based our analysis on a dynamical system (10) that approximates the stochastic density process when the population ceiling is large.
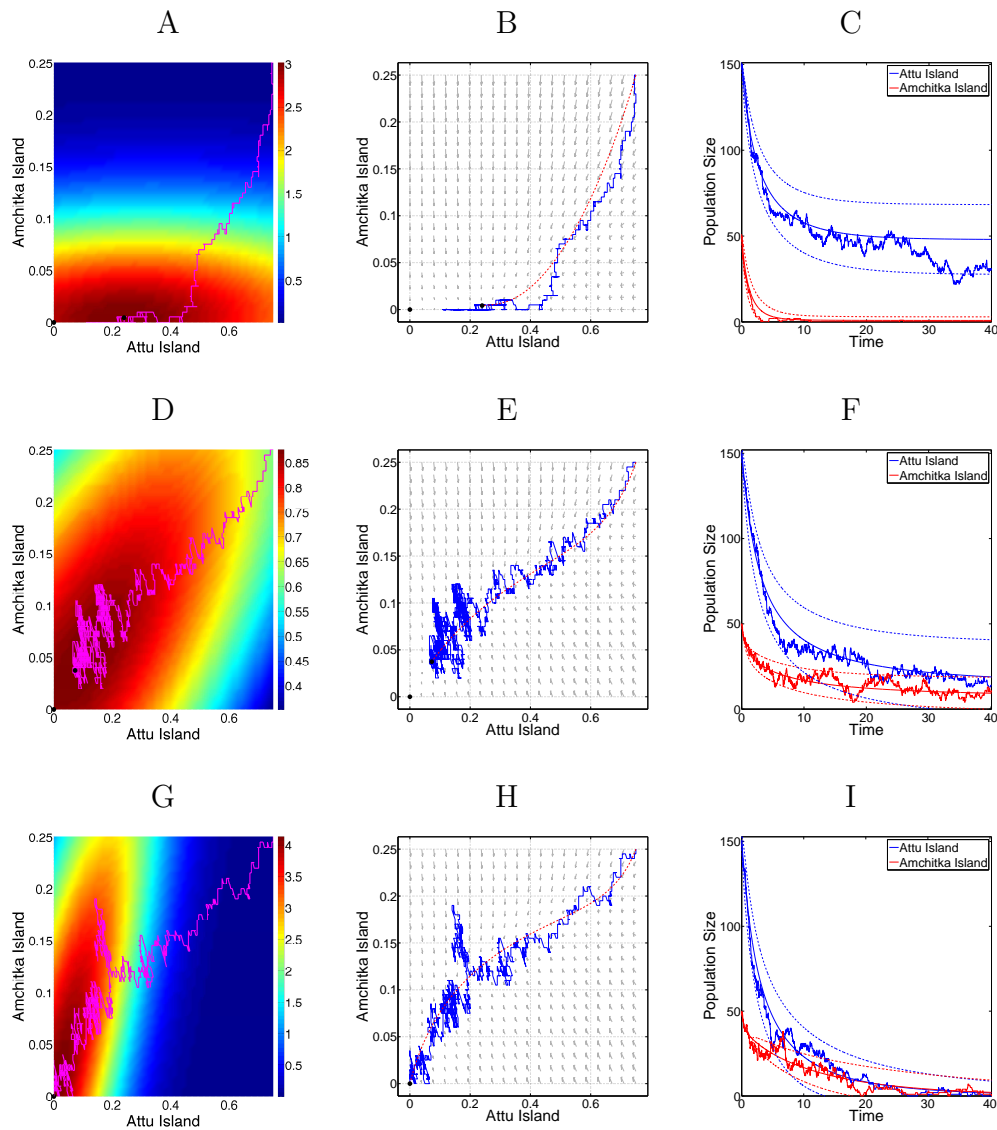
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Figure 5: An illustration of the effect the migration rates and the connectivity have on the persistence of a metapopulation with a population ceiling of 200 sea otters at Attu and Amchitka Islands. For the three cases mentioned in the text, A, D and G illustrate contours of the distribution of the two–dimensional approximating Gaussian diffusion (Theorem Appendix A.1) at $t = 40$ years, together with one realisation of the metapopulation model; B, E and H show the same realisation (solid blue line) on a phase plane diagram together with the deterministic trajectory (10) (dotted red line); and C, F and I show this realisation and the deterministic trajectory along with ± 2 standard deviations (dotted lines) determined from the distribution of the approximating Gaussian diffusion.

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Our theorems combine to give a detailed description of the long term behaviour of the model. Under Assumption (E), the long term behaviour of the system is completely described; inequality (13) determines the extinction or persistence of the metapopulation. When Assumption (E) does not hold, however, the metapopulation may display more complex behaviour.

The discovery of an Allee effect in the two–patch metapopulation model is unexpected as the birth rate functions for each patch are strictly decreasing. It appears that the Allee effect arises as a result of a large variation in the migration rates which depends on the population density of the patches. For a metapopulation where the two patches are of greatly different sizes, a high population density on the smaller patch allows the population to become established on the larger patch as emigration from the larger patch is reduced to a very low level. We note that the presence of an Allee effect in a metapopulation has important implications for the design of conservation strategies. Conservation targets need to be set taking into account the critical threshold below which the metapopulation goes extinct [25, section 5.1.4]. Similarly, for the successful reintroduction of a species, the release size needs to be sufficiently large for the population density to exceed the critical threshold [37]. The Allee effect can also be exploited to create more efficient strategies for managing invasive pests [38].

We also discovered the possibility of three nonzero fixed points in the two–patch model when the zero fixed point is unstable. For the J–patch system, there are $2^J - 1$ possible nonzero fixed points, which, if all are contained in E, would result in the Allee effect occurring at many intermediate population sizes. Although the perturbation analysis conducted for the two–patch model could be generalised to larger number of patches, the expressions involved quickly become cumbersome. Thus, a different approach will be required to improve our understanding of the Allee effect in this model.

The veracity of our conclusions is dependent on how well the stochastic model (4) – (6) is approximated by the dynamical system (10). We mentioned briefly in Section 3 that the accuracy could be quantified using the results of [26]. However, it is important to note

that, in general, the accuracy of the dynamical systems approximation deteriorates near the extinction state [41, 42]. Therefore, alternative methods might be needed to improve our understanding of the stochastic metapopulation model near extinction.

One aspect of population dynamics that our model excludes, but has been incorporated in other models [19, 43, 17], is the potential for catastrophes. A catastrophe occurs when every individual on a given patch dies instantly or when all individuals on a patch are subject to a higher death rate over some small period of time. An obvious extension then would be to include catastrophes. Doing so would increase the chance an individual dies, hence the birth rate required for the metapopulation to survive would naturally have to be higher. One way to introduce catastrophes into our model would be to randomly switch between two sets of parameters where one set includes a much higher death rate. However, if catastrophes were introduced, a deterministic approximation could not be used to study the stochastic model, since catastrophes are inherently random events and affect a large number of individuals. These two aspects are not approximated well by a deterministic system, even in the limit as population ceiling N gets large. However, the behaviour of the metapopulation between catastrophes would remain unchanged. A piecewise deterministic approximation to a model including catastrophes might be obtained using the functional limit laws of Franz et al. [44].

Appendix A.

As stated earlier, Theorem 3.1 does not provide information concerning the stochastic fluctuations about the deterministic trajectory. Therefore, we appeal to Theorem 3.2 of [24], the analogue of Theorems 3.1 and 3.5 of Kurtz [45] for asymptotically density dependent families. To this end define $G(x) = (g_{ij}(x))$ by

$$g_{ij}(x) = -\hat{\phi}_i(x_i)\lambda_{ij}\left(1 - \frac{x_j}{M_j}\right) - \hat{\phi}_j(x_j)\lambda_{ji}\left(1 - \frac{x_i}{M_i}\right), \qquad \text{for } j \neq i,$$

and

$$g_{ii}(x) = \nu_i M_i + \left(b_i\left(\frac{x_i}{M_i}\right) + d_i - \nu_i\right)x_i + \hat{\phi}_i(x_i)$$
$$+ \sum_{j \neq i, 0}\left(\hat{\phi}_j(x_j)\lambda_{ji}\left(1 - \frac{x_i}{M_i}\right) - \hat{\phi}_i(x_i)\lambda_{ij}\frac{x_j}{M_j}\right), \qquad \text{for all } i.$$

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It can be seen that G is bounded and uniformly continuous if $\hat{\phi}_i$ has this property for all i, while F has uniformly continuous first partial derivatives whenever $\hat{\phi}_i$ has this property for all i. Noting that the Jacobian $H(x) = (h_{ij}(x))$ of F is given by

$$h_{ij}(x) = \hat{\phi}'_j(x_j)\lambda_{ji} + \hat{\phi}_i(x_i)\frac{\lambda_{ij}}{M_j} - \hat{\phi}'_j(x_j)\frac{\lambda_{ji}x_i}{M_i}, \quad \text{for } j \neq i,$$

and

$$h_{ii}(x) = b_i\left(\frac{x_i}{M_i}\right) + \frac{x_i}{M_i}b'_i\left(\frac{x_i}{M_i}\right) - \nu_i - d_i - \hat{\phi}'_i(x_i)\left(\lambda_{i0} + \sum_{j \neq i}\lambda_{ij}\left(1 - \frac{x_j}{M_j}\right)\right) - \sum_{j \neq i}\hat{\phi}_j(x_j)\frac{\lambda_{ji}}{M_i},$$

for all i, we can apply Theorem 3.2 of [24] to show that the fluctuations of $X_N(t)$ about the deterministic trajectory follow a Gaussian diffusion.

Theorem Appendix A.1. *Assume the conditions of Theorem 3.1 hold. Assume also that $\hat{\phi}_i$ has uniformly continuous first partial derivatives and*

$$\lim_{N \to \infty} \sqrt{N}\left(X_N(0) - x_0\right) = z.$$

Then the family of processes $\{Z_N(t)\}$, defined by

$$Z_N(s) = \sqrt{N}\left(X_N(s) - x(s, x_0)\right), \quad 0 \leq s \leq t,$$

converges weakly in $D[0, t]$ to a Gaussian diffusion $Z(t)$ with initial value $Z(0) = z$ and characteristic function $\psi = \psi(t, \theta)$ that satisfies

$$\frac{\partial\psi(t,\theta)}{\partial t} = -\frac{1}{2}\sum_{j,k}\theta_j g_{jk}(x(t))\theta_k\psi(t,\theta) + \sum_{j,k}\theta_j\frac{\partial F_j(x(t))}{\partial x_k}\frac{\partial\psi(t,\theta)}{\partial\theta_k}.$$

The scaled fluctuations $Z_N(t)$ about the deterministic trajectory can thus be approximated by a Gaussian distribution with mean $\mathbb{E}\left(Z(t)\right) = M(t)z$ and covariance matrix $\text{Cov}(Z(t)) = \Sigma(t)$, where

$$\Sigma(t) = M(t)\left(\int_0^t M(u)^{-1}G(x(u, x_0))(M(u)^{-1})^T du\right)M(t)^T$$

and

$$M(t) = \exp\left(\int_0^t H(u)du\right).$$

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The covariance matrix of $Z(t)$ can be evaluated explicitly only in some simple cases. However, since populations are often observed in equilibrium, it makes sense to assume that the initial value x_0 is a fixed point x^* of F. In that case, we may appeal to results of Barbour [46, 47] which show that the fluctuations around x^* are approximated by an Ornstein-Uhlenbeck process.

Theorem Appendix A.2. *Assume the conditions of Theorem Appendix A.1 hold and*

$$\lim_{N \to \infty} \sqrt{N} \left(X_N(0) - x^* \right) = z.$$

The family of processes $\{Z_N(t)\}$, defined by

$$Z_N(s) = \sqrt{N} \left(X_N(s) - x^* \right), \quad 0 \leq s \leq t,$$

converges weakly in $D[0, t]$ to an Ornstein-Uhlenbeck process $Z(t)$ with initial value $Z(0) = z$, local drift matrix $H = \nabla F(x^*)$ and local covariance matrix $G(x^*)$. $Z(t)$ follows a Gaussian diffusion with mean $\mu(t) = e^{Ht} z$ and covariance matrix

$$\Sigma(t) = e^{Ht} \left(\int_0^t e^{-Hs} G(x^*) e^{-H^T s} ds \right) e^{H^T t}.$$

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