

INTERACTION BETWEEN HABITAT QUALITY AND AN ALLEE-LIKE EFFECT IN METAPOPOPULATIONS

R. McVINISH and P.K. POLLETT

School of Mathematics and Physics, University of Queensland

ABSTRACT.

We construct a stochastic patch occupancy metapopulation model that incorporates variation in habitat quality and an Allee-like effect. Using some basic results from stochastic ordering, we investigate the effect of habitat degradation on the persistence of the metapopulation. In particular, we show that for a metapopulation with Allee-like effect habitat degradation can cause a dramatic decrease in the level of persistence while in the absence of an Allee-like effect this decrease is more gradual.

Key words: Allee effect, habitat destruction, metapopulation, SPOM.

MSC 2010: 92D40; 60J10

1. INTRODUCTION

Many species exist as a collection of local populations occupying spatially distinct habitat patches. Such a collection of local populations is called a metapopulation. Metapopulations are constantly changing due to the processes of local extinction and colonisation occurring at each habitat patch. The primary focus in the study of metapopulations is to determine conditions under which the metapopulation may persist. The persistence of a metapopulation is determined by various factors associated with the landscape and the dynamics of the population.

One important factor of the landscape is habitat quality. Following Hall et al. [7] and Mortelliti et al. [17], we consider habitat quality to be the ability of the environment to provide conditions appropriate for individual and population persistence. We might therefore view the rate or probability of local extinction as reflecting the habitat quality of a patch. In this sense, the classical Levins metapopulation model assumes the habitat

RM and PKP are supported by the Australian Research Council (Discovery grant DP110101929 and Center of Excellence for Mathematics and Statistics of Complex Systems)

quality is homogeneous across the landscape. However, real metapopulations tend to display variation in the habitat quality. The study of the Glanville fritillary (*Melitaea cinxia*) by Hanski et al. [10] provides one example. Mortelliti et al. [17] gives an overview of the role of habitat quality in metapopulations.

A number of mathematical metapopulation models have been proposed that are able to incorporate heterogeneity in the habitat quality of patches. The incidence function model [8] and the spatially realistic Levins model [9] are both able to closely reflect the ecological reality by incorporating information concerning the distance between habitat patches and patch area as well as variation in habitat quality. However, these models are complex to analyse; their behaviour being determined by the leading eigenvalue of $n \times n$ matrices where n is the number of patches in the metapopulation [19, 11]. Gyllenberg and Hanski [6] proposed a simpler partial differential equation model that incorporates variation in habitat quality and a ‘rescue effect’, an effect which decreases the rate of extinction for well connected patches, and derived simple conditions for persistence. McVinish and Pollett [15] consider a discrete time Markov chain model that incorporates variation in habitat quality through patch dependent local extinction probabilities but ignores the locations of the patches in the landscape. Models such as these are especially important when considering habitat degradation and destruction since such changes are unlikely to occur uniformly across the landscape.

In addition to habitat quality, the persistence of a metapopulation is affected by its dynamical properties. In this paper we are concerned with one such property called an Allee-like effect. This term is borrowed from population biology where the Allee effect refers to populations exhibiting an increasing per capita growth rate at low population density levels. If the per capita growth rate is initially negative the population will exhibit a critical threshold below which the population goes extinct. Courchamp et al. [4] provide a detailed discussion of the Allee effect in ecology. For metapopulations, an Allee-like effect refers to a metapopulation exhibiting a similar behaviour. Amarasekare [1] summarises some of the evidence supporting the operation of an Allee-like effect in real metapopulations and proposes a modification of the Levins model which exhibits this phenomenon (see also Courchamp et al. [4] pages 103-105). Note that, as in the Levins model, Amarasekare’s model assumes homogeneous habitat quality. Hui and Li [13] extended this model to incorporate both a ‘rescue effect’ and an ‘overcrowding effect’

while Zhou et al. [22] considered a two species version of the model. Although each of these three papers consider the effect of habitat destruction, the assumption of homogeneous patch characteristics limited their analyses to considering either complete destruction of certain patches or a common reduction in the survival rates for all patches.

In this paper, we examine the effect of habitat degradation on a metapopulation exhibiting an Allee-like effect using the metapopulation model introduced in McVinish and Pollett [15]. As stated earlier, this is a discrete time Markov chain and although it difficult to analyse directly, it can be well approximated by a simpler deterministic process when the number of habitat patches is large. In Section 2 of this paper we review this model and provide some new results on the behaviour of the approximating deterministic process. In Section 3 we show how this model can be modified to incorporate an Allee-like effect by imposing certain conditions on the colonisation process. In Section 4 the deterministic approximation is used to study the effect that habitat degradation has on the persistence of the metapopulation. It is demonstrated that even a small amount of habitat degradation in a metapopulation exhibiting an Allee-like effect can cause it to go extinct regardless of the original level of persistence. This can be contrasted with a metapopulation that does not exhibit an Allee-like effect where a small change to the habitat quality will result in only a small change to the level of persistence of the metapopulation. Therefore, we believe that metapopulations exhibiting an Allee-like effect are in much greater need of protection from habitat degradation and destruction. Some discussion of possible extensions to this work is given in Section 5. The proofs of the new results in this paper are given in A.

2. A METAPOPOPULATION MODEL

In this section, we summarise the model studied in [15]. This model is an example of a stochastic patch occupancy model (SPOM) as only the presence or absence of the species of interest is noted for each habitat patch and not the size or structure of the population at the habitat patch. Consider a metapopulation comprised of n habitat patches and let $X_t^{(n)}$ indicate the state of this metapopulation at time t where $X_t^{(n)} = (X_{1,t}^{(n)}, \dots, X_{n,t}^{(n)})$ with

$$X_{i,t}^{(n)} = \begin{cases} 1, & \text{if habitat patch } i \text{ is occupied at time } t, \\ 0, & \text{otherwise.} \end{cases} \quad (2.1)$$

Between observations, the metapopulation undergoes a series of colonisation and extinction events. In this model, these events are separated into distinct phases as in [12] and [3]. First, a colonisation phase occurs during which unoccupied patches are colonised by individuals from the occupied patches. The colonisation events are assumed to be independent of one another and the probability of an unoccupied patch being successfully colonised during this phase is given by a function, f , of the proportion of occupied patches in the metapopulation. The function f is called the colonisation function and satisfies the following assumption;

- (A) The colonisation function $f : [0, 1] \mapsto [0, 1]$ is an increasing, concave function such that $f(0) = 0$ and $f'(0) > 0$.

The assumption that $f(0) = 0$ means that once all habitat patches are unoccupied, they cannot be recolonised from some outside source and the metapopulation is extinct. Concave colonisation functions such as $f(x) = 1 - \exp(-\beta x)$, $\beta > 0$ [12] are commonly used, but non-concave functions are also relevant. The case of non-concave colonisation functions will be studied in the next section. Although this type of colonisation process ignores the connectivity and distances between habitat patches, it facilitates the analysis of the model. During the extinction phase, the local population at habitat patch i goes extinct with probability $1 - s_i$ independently of the other patches. We call s_i the survival probability at patch i . Differences in survival probabilities between patches can arise simply due to differences in patch area (an assumption used, for example, in Moilanen [14]), though other factors may have greater importance for population survival such as the abundance of food and shelter and the absence of predators. This is the case for the ragwort plant *Senecio jacobaea* [20].

Mathematically, the metapopulation model $\{X_t^{(n)}\}_{t=0}^T$ is a discrete time Markov chain. To describe the transitions, let $B(m, p)$ denote the binomial distribution with parameters $m \in \{0, 1\}$ and $p \in [0, 1]$. The transitions of $X_t^{(n)}$ are given by

$$X_{i,t+1}^{(n)} \sim B(X_{i,t}^{(n)}, s_i) + B\left(1 - X_{i,t}^{(n)}, s_i f\left(n^{-1} \sum_{j=1}^n X_{j,t}^{(n)}\right)\right). \quad (2.2)$$

The first term on the right hand side of (2.2) models a population occupying a habitat patch surviving the extinction phase, while the second term models an unoccupied patch being colonised and then the occupying population surviving the extinction phase. The

complexity of the model prevents an exact treatment. Instead we consider a deterministic approximation which is valid when the number of habitat patches is large. There is a large literature describing this type of approximation for continuous time Markov chains (see Darling and Norris [5] and references therein). To construct the deterministic approximation of the metapopulation model, we impose the following assumption on the survival probabilities and initial state of the metapopulation.

(B) There exists a probability measure σ and deterministic sequence $\{d(0, k)\}_{k=0}^{\infty}$ such that

$$n^{-1} \sum_{i=1}^n s_i^k \xrightarrow{p} \bar{s}_k := \int_0^1 \lambda^k \sigma(d\lambda), \quad \text{and} \quad n^{-1} \sum_{i=1}^n s_i^k X_{i,0}^{(n)} \xrightarrow{p} d(0, k) \quad (2.3)$$

for all $k = 0, 1, \dots$

We call σ the survival distribution. Assumption (B) will hold if, for example, the s_i are independent and identically distributed random variables with distribution σ and if, given the s_i , the $X_{i,0}^{(n)}$ are independent Bernoulli random variables with $P(X_{i,0}^{(n)} = 1 | s_i) = p(s_i)$ for some function p .

Theorem 2.1 (Theorem 2.1 of McVinish and Pollett [15]). *Suppose that (B) holds. Then for all $k = 0, 1, \dots$ and all $t = 0, 1, 2, \dots$*

$$n^{-1} \sum_{i=1}^n s_i^k X_{i,t}^{(n)} \xrightarrow{p} d(t, k), \quad (2.4)$$

where

$$d(t+1, k) = d(t, k+1) + f(d(t, 0)) (\bar{s}_{k+1} - d(t, k+1)). \quad (2.5)$$

We are primarily interested in the sequence $\{d(t, 0)\}_{t=0}^T$ which gives the limiting proportion of occupied patches in the metapopulation. However, the other values of $d(t, k)$ do provide some useful information. For example, given t , the sequence $\{d(t, k)/d(t, 0)\}_{k=1}^{\infty}$ can be interpreted as the moments of the distribution of the survival probabilities of occupied patches.

To better understand the infinite system of difference equations (2.5), we examine its equilibrium points and their stability. A sequence $\{d(k)\}_{k=0}^{\infty}$ is an equilibrium point of (2.5) if it satisfies

$$d(k) = d(k+1) + f(d(0)) (\bar{s}_{k+1} - d(k+1)). \quad (2.6)$$

It is said to be stable if for all initial conditions $\{d(0, k)\}_{k=0}^{\infty}$ in a sufficiently small neighbourhood of $\{d(k)\}_{k=0}^{\infty}$

$$\lim_{t \rightarrow \infty} d(t; k) = d(k), \quad (2.7)$$

for all $k \geq 0$. To make this definition precise we need some additional mathematical background. A sequence $\{c_k\}_{k=0}^{\infty}$ is said to be completely monotone if $(-1)^m \Delta^m c_n \geq 0$ for all $n, m \geq 0$ where Δ is the difference operator. One can show from the limit (2.4) that, for each t , $\{d(t, k)\}_{k=0}^{\infty}$ is completely monotone, hence there exists a unique measure μ_t whose moments are given by $\{d(t, k)\}_{k=0}^{\infty}$ (see Theorem 4a in chapter III of Widder [21]). This is true also of the equilibrium points. A neighbourhood of the equilibrium point is interpreted as a weak neighbourhood of its associated measure. The limit (2.7) implies the weak convergence of μ_t to the measure associated with the equilibrium point. See Billingsley [2, chapter 1, section 2] for details on weak neighbourhoods of measures and weak convergence. If the limit (2.7) does not hold then the equilibrium point is called unstable. If the limit (2.7) holds for all initial conditions, then the equilibrium is said to be globally stable.

The stable equilibrium point(s) of the system will provide an approximation of the long run proportion of occupied patches in the metapopulation. The following theorem gives a complete description of the equilibrium points of (2.5) and their stability.

Theorem 2.2. *Suppose that (A) holds. The equilibrium points of the recursion (2.5) are given by*

$$d(k) = \int_0^1 \frac{f(\psi)\lambda^{k+1}}{1 - \lambda + f(\psi)\lambda} \sigma(d\lambda), \quad (2.8)$$

where ψ solves

$$\psi = R_{\sigma}(\psi) := \int_0^1 \frac{f(\psi)\lambda}{1 - \lambda + f(\psi)\lambda} \sigma(d\lambda). \quad (2.9)$$

The extinction state, $d(k) \equiv 0$, is the unique equilibrium point of (2.5) and is globally stable if and only if

$$f'(0) \int_0^1 \frac{\lambda}{1 - \lambda} \sigma(d\lambda) \leq 1. \quad (2.10)$$

If inequality (2.10) does not hold, then the recursion (2.5) has two equilibrium points of which one is $d(k) \equiv 0$. Furthermore, if $d(0; 0) > 0$ then, for all k $\lim_{t \rightarrow \infty} d(t; k) = d(k) > 0$.

The fixed points of the recursion (2.5) were identified in Theorem 2.2 in [15]. The local stability of the zero fixed point when inequality (2.10) holds and the local stability of the non-zero fixed point when inequality (2.10) does not hold were given in Theorem 2.3 in [15]. The theorem stated above is a considerable improvement on those results. From this theorem we see that the zero equilibrium point is unstable if inequality (2.10) does not hold. This will be important for our discussion of the Allee-like effect. A proof of Theorem 2.2 is given in the appendix.

3. INCORPORATING AN ALLEE-LIKE EFFECT

An Allee-like effect for metapopulations can be defined as the metapopulation exhibiting an increasing per patch growth rate at low levels of occupation. If the per patch growth rate is negative for sufficiently low levels of occupation, then the metapopulation will exhibit a threshold, that is, below a certain level of occupation the metapopulation will go extinct and above this level of occupation the metapopulation will persist. When a threshold is present, the effect is called a strong Allee-like effect. See [4, chapter 1] for an overview of the Allee effect. As we shall only be concerned with this case, we shall simply call it an Allee-like effect.

In mathematical terms, the Allee-like effect means that zero, the extinction state, is a locally stable equilibrium point of the system (2.5). Furthermore, at least one non-zero stable equilibrium point exists. From Theorem 2.2 we see that our model, as formulated in Section 2, cannot display the Allee-like effect; either the extinction state is globally stable or it is unstable. To allow for the possibility of an Allee-like effect we need to modify Assumption (A).

(A') The colonisation function $f : [0, 1] \mapsto [0, 1]$ is an increasing differentiable function such that $f(0) = 0$ and satisfying the inequality

$$\frac{f(x)}{x} \int_0^1 \frac{\lambda}{1-\lambda} \sigma(d\lambda) < 1 \quad (3.11)$$

for all sufficiently small $x > 0$.

Note that if f is differentiable and concave in a neighbourhood of zero then inequality (3.11) is equivalent to inequality (2.10).

We now consider the behaviour of the equilibrium points of our modified metapopulation model. Under assumption (A'), the fixed points of (2.5) are still given by equations

(2.8) and (2.9), however the number of solutions to (2.9) cannot be easily determined. To establish that our modified model exhibits an Allee-like effect we need to examine the stability of the zero fixed point. The following theorem establishes a condition on the initial state of the metapopulation under which the metapopulation goes extinct and thereby showing that the extinction state is at least locally stable under Assumption (A').

Theorem 3.1. *Assume that equation (2.9) has at least one non-zero solution. Let x^* be the smallest $x > 0$ satisfying*

$$f(x) \int_0^1 \frac{\lambda}{1-\lambda} \sigma(d\lambda) = x. \quad (3.12)$$

If $\sum_{k=0}^{\infty} d(0; k) < x^$ then $\lim_{t \rightarrow \infty} d(t; 0) \rightarrow 0$.*

The proof of Theorem 3.1 is given in the appendix. It is important to note that the condition in Theorem 3.1 concerns not only the proportion of occupied patches in the metapopulation but also the quality of those occupied patches. If the survival probabilities are bounded by s^* then we can apply Theorem 3.1 to conclude that the metapopulation will go extinct if the initial proportion of occupied patches is less than $x^*(1 - s^*)$.

As in the original model, the stability of the non-zero equilibrium points is of interest as they determine the possibility of the metapopulation persisting over long time periods. The stability of the non-zero equilibrium points is determined by the following theorem.

Theorem 3.2. *Let ψ^* be a non-zero solution to (2.9). If $R'_\sigma(\psi^*) < 1$ then the corresponding equilibrium point given by equation (2.8) is stable. If $R'_\sigma(\psi^*) > 1$ then the corresponding equilibrium point is unstable.*

The proof of Theorem 3.2 for $R'_\sigma(\psi^*) < 1$ follows the same arguments as in the proof of case (i) of Theorem 2.3 in [15]. The proof for $R'_\sigma(\psi^*) > 1$ is given in the appendix. Note that this theorem does not cover the case where $R'_\sigma(\psi^*) = 1$. That case will require a more detailed analysis.

Unfortunately, we have not been able to provide a partitioning of the initial states of the metapopulation into their corresponding limiting equilibrium points as was achieved by Amarasekare [1] for the much simpler extended Levins model. In particular, Theorem 3.1 only provides a lower bound on the threshold for the metapopulation. It does not provide a condition on the initial state which ensures that the metapopulation approaches a non-zero equilibrium.

4. HABITAT DESTRUCTION AND DEGRADATION

Metapopulation models have often been used to study the effect of the habitat destruction on the behaviour of the metapopulation and, in particular, its effect on the equilibrium level. Most of these models were only able to reveal the effect of complete destruction of a certain proportion of the habitat patches (see, for example Amarasekare [1], Hill and Caswell [12], Zhou et al. [22]). One notable exception is the model studied by Gyllenberg and Hanski [6] which incorporated patch quality and studied the interaction between habitat degradation and the rescue effect. Here, we consider a varying degree of habitat degradation at each habitat patch. Habitat degradation at patch i is modelled by a decrease in the survival probability $s_i \mapsto s'_i < s_i$. Complete destruction of patch i is indicated by $s_i \mapsto 0$. The quality of the habitats in two metapopulations can be compared using the theory of stochastic ordering [18]. Let σ_1 and σ_2 be two distributions on $[0, 1)$. We write $\sigma_1 \leq \sigma_2$ if for all $x \in [0, 1)$, $\sigma_1((x, 1)) \leq \sigma_2((x, 1))$. We write $\sigma_1 < \sigma_2$ if $\sigma_1 \leq \sigma_2$ and if for some $x \in [0, 1)$, $\sigma_1((x, 1)) < \sigma_2((x, 1))$. The following two properties are important for our application (Theorems 1.28 and 1.29 in Müller and Stoyan [18]):

(i) If $\sigma_1 \leq \sigma_2$, then for any increasing function u ,

$$\int u(\lambda)\sigma_1(d\lambda) \leq \int u(\lambda)\sigma_2(d\lambda).$$

(ii) If $\sigma_1 \leq \sigma_2$ and

$$\int u(\lambda)\sigma_1(d\lambda) = \int u(\lambda)\sigma_2(d\lambda)$$

for some strictly increasing function, then $\sigma_1 = \sigma_2$.

First note that the integrand in equation (2.9) is increasing under both assumption (A) and (A'). Therefore, if $\sigma_1 < \sigma_2$ then for all $\psi \in (0, 1]$, $R_{\sigma_1}(\psi) < R_{\sigma_2}(\psi)$. Furthermore, we note that if σ_m converges weakly to σ then for all ψ , $R_{\sigma_m}(\psi) \rightarrow R_{\sigma}(\psi)$. In the absence of an Allee-like effect, that is under assumption (A), these properties imply that the non-zero equilibrium point ψ^* is a continuous, non-increasing function of σ . In other words, in the absence of an Allee-like effect, degrading the habitat will result in a gradual decrease of the equilibrium level. This point is illustrated in Figure 1 (Left).

The effect of habitat degradation can be more dramatic in the presence of an Allee-like effect. Suppose that σ^* satisfies $R_{\sigma^*}(\psi) \leq \psi$ for all $\psi \in [0, 1]$ and for some $\psi^* > 0$, $R_{\sigma^*}(\psi^*) = \psi^*$. The only equilibrium point of a metapopulation with survival

FIGURE 1. The functions $R_\sigma(\psi)$ are plotted for survival distributions $\text{Beta}(\alpha, 2)$ with various values of α . The intersection of the curve $R_\sigma(\psi)$ with the straight line gives the equilibrium levels of the metapopulations. Note that if $\alpha_1 < \alpha_2$ then $\text{Beta}(\alpha_1, 2) < \text{Beta}(\alpha_2, 2)$ in the stochastic ordering. Left: No Allee-like effect. The colonisation function is $f(x) = 0.7x$ and $\alpha = 8, 6, 4, 2, 1$. Right: Allee-like effect. A non-concave colonisation function is used with $f(1) = 0.7$ and $\alpha = 8, 5.68, 4$.

distribution $\sigma < \sigma^*$ is the extinction state $\psi^* = 0$. On the other hand, a metapopulation with survival distribution σ such that $\sigma^* < \sigma$ has at least one non-zero stable equilibrium point. This point is illustrated in Figure 1 (Right).

Finally, we note that equilibrium points with $R'_\sigma(\psi^*) > 1$ may increase under habitat degradation. However, Theorem 3 states that such equilibrium points are unstable and hence do not provide an approximation to the long run proportion of occupied patches in the metapopulation.

5. DISCUSSION

Previous metapopulation models incorporating an Allee-like effect have been based on Levins's model [1, 13, 22]. Therefore, they are unable to incorporate variation in habitat patch characteristics. We considered a variation of the metapopulation model of McVinish and Pollett [15] which incorporates both the Allee-like effect and variation in habitat patch characteristics. This model was used to compare the effects of habitat degradation on metapopulations both with and without an Allee-like effect. It was demonstrated that for metapopulations with an Allee-like effect even a small amount of habitat degradation can have catastrophic consequences.

We conjecture that the threshold should be given by the smallest non-zero equilibrium point which we will denote by $d_T(k)$. Any initial state $d(0; k)$ which dominates this equilibrium point, that is, for which $d_T(k) \leq d(0; k)$ for all $k \geq 0$, will lead to a metapopulation that persists at a non-zero level of occupation. This follows from property (i) in the proof of Theorem 2.2 (see A.1). We have not been able to show that any initial state that is dominated by this equilibrium, $d(0; k) \leq d_T(k)$ for all $k \geq 0$, would result in the

metapopulation converging to the extinction state. However, it is relatively simple to verify that this is true for the case where all patches have the same survival probability.

Finally, we remark that the analysis of this paper has focused on the behaviour of the deterministic limit of the metapopulation model. A central limit theorem for an extended version of our metapopulation model is given in McVinish and Pollett [16]. It may be fruitful to investigate the effects of habitat destruction and degradation on the metapopulation using the more precise limit theory described in that paper.

APPENDIX A. PROOF OF THEOREMS

A.1. Proof of Theorem 2.2. To prove this theorem we first need to prove the following three properties of the recursion (2.5):

- (i) If $d_1(0; k) \leq d_2(0; k)$ for all $k \geq 0$ then $d_1(t; k) \leq d_2(t; k)$ for all $t \geq 0$ and all $k \geq 0$. *Proof.* This property is proved by induction. Suppose that for some T , $d_1(T; k) \leq d_2(T; k)$ for all $k \geq 0$. Then

$$\begin{aligned} d_1(T+1; k) &= (1 - f(d_1(T; 0))) d_1(T; k+1) + f(d_1(T; 0)) \bar{s}_{k+1} \\ &\leq (1 - f(d_1(T; 0))) d_2(T; k+1) + f(d_1(T; 0)) \bar{s}_{k+1} \\ &\leq (1 - f(d_2(T; 0))) d_2(T; k+1) + f(d_2(T; 0)) \bar{s}_{k+1} \\ &\leq d_2(T+1; k), \end{aligned}$$

where the second last inequality follows as f is increasing and $d(t; k) \leq \bar{s}_k$ for any $t, k \geq 0$. This completes the proof.

Assume that inequality (2.10) does not hold and let $d(k)$ denote the non-zero equilibrium point.

- (ii) If $d(0; 0) > 0$ then there exists an $\epsilon \in (0, 1)$ such that $d(1; k) \geq \epsilon d(k)$. *Proof.* From the recursion (2.5), $d(1; k) \geq f(d(0; 0)) \bar{s}_{k+1}$ for all $k \geq 0$. As $f(\psi^*)(1 - \lambda + \lambda f(\psi^*))^{-1} \leq 1$, it follows from equation (2.8) that $\bar{s}_{k+1} \geq d(k)$ for all $k \geq 0$. This completes the proof.

(iii) If $d(0; k) \geq \epsilon d(k)$ for some $\epsilon \in (0, 1)$ and all $k \geq 0$ then $d(1; k) \geq \epsilon d(k)$ for all $k \geq 0$. *Proof.* From recursion (2.5),

$$\begin{aligned}
 d(1; k) &= (1 - f(d(0; 0))) d(0; k + 1) + f(d(0; 0)) \bar{s}_{k+1} \\
 &\geq (1 - f(d(0; 0))) \epsilon d(k + 1) + f(d(0; 0)) \bar{s}_{k+1} \\
 &\geq (1 - f(\epsilon d(0))) \epsilon d(k + 1) + f(\epsilon d(0)) \bar{s}_{k+1} \\
 &\geq (1 - \epsilon f(d(0))) \epsilon d(k + 1) + \epsilon f(d(0)) \bar{s}_{k+1} \\
 &\geq (1 - f(d(0))) \epsilon d(k + 1) + \epsilon f(d(0)) \bar{s}_{k+1} = \epsilon d(k),
 \end{aligned}$$

where the second last inequality follows from the concavity of f , that is, $f(\epsilon x) \geq \epsilon f(x)$. This completes the proof.

Having demonstrated properties (i) – (iii), we now prove that if inequality (2.10) holds then the zero equilibrium point is globally stable. Consider the recursion (2.5) with initial condition $d(0; k) = \bar{s}_k$. If we can show that $\lim_{t \rightarrow \infty} d(t; k) = 0$ then, by property (i), the recursion with any other initial condition must also converge to zero. Hence, we will have established that the zero equilibrium is globally stable. Now $d(1; k) \leq \bar{s}_k$, so by property (i) $d(t; k)$ is decreasing in t . As the $d(t; k)$ are non-negative, the limit as $t \rightarrow \infty$ exists. Let $\tilde{d}(k) = \lim_{t \rightarrow \infty} d(t; k)$. As f is a continuous function, it follows that $\tilde{d}(k)$ must be a fixed point of the recursion (2.5). As the zero fixed point is the only fixed point assuming inequality (2.10) holds, $\tilde{d}(k) = 0$.

Now suppose that inequality (2.10) does not hold. By property (ii), if $d(0, 0) > 0$ then there exists an $\epsilon \in (0, 1)$ such that $d(1; k) \geq \epsilon d(k)$ for all $k \geq 0$. Let $d_L(0; k) = \epsilon d(k)$ and $d_U(0; k) = \bar{s}_k$. Clearly, $d_L(0; k) \leq d(1; k) \leq d_U(0; k)$ and by property (i)

$$\epsilon d(k) \leq d_L(t; k) \leq d(t + 1; k) \leq d_U(t; k) \leq \bar{s}_k \tag{A.13}$$

for all t . Since $d_U(1; k) \leq \bar{s}_k$ it follows from property (i) that $d_U(t; k)$ is decreasing in t for all $k \geq 0$. Similarly, from property (iii) $d_L(1; k) \geq d_L(0; k)$ and hence property (i) implies that $d_L(t; k)$ is increasing in t for all $k \geq 0$. Both $d_U(t; k)$ and $d_L(t; k)$ must converge to limiting values $\tilde{d}_U(k)$ and $\tilde{d}_L(k)$ that are fixed points of the recursion. From inequality (A.13), $\epsilon d(k) \leq \tilde{d}_L(k) \leq \tilde{d}_U(k)$. As the non-zero fixed point is unique, it follows that $d(k) = \tilde{d}_L(k) = \tilde{d}_U(k)$. Finally, from inequality (A.13) we see that $\lim_{t \rightarrow \infty} d(t; k) = d(k)$ for any initial condition satisfying $d(0; 0) > 0$. This completes the proof.

A.2. Proof of Theorem 3.1. Clearly,

$$R_\sigma(\psi) \leq f(\psi) \int_0^1 \frac{\lambda}{1-\lambda} \sigma(d\lambda), \quad \text{for all } \psi \in [0, 1].$$

Therefore, if equation (2.9) has a non-zero solution and Assumption (A') holds then there exists an $x^* > 0$ satisfying equation (3.12).

Now let $\phi_t = \sum_{k=0}^{\infty} d(t; k)$. We aim to show that if $\phi_0 < x^*$ then $\lim_{t \rightarrow \infty} d(t; 0) = 0$. If inequality (2.10) holds then ϕ_t is finite since

$$\phi_t = \sum_{k=0}^{\infty} d(t; k) \leq \sum_{k=0}^{\infty} \bar{s}_k = 1 + \int_0^1 \frac{\lambda}{1-\lambda} \sigma(d\lambda) < \infty.$$

From recursion (2.5) we have

$$\phi_{t+1} = \phi_t + d(t; 0) \left(\frac{f(d(t; 0))}{d(t; 0)} \int_0^1 \frac{\lambda}{1-\lambda} \sigma(d\lambda) - 1 \right) + f(d(t; 0)) (d(t; 0) - \phi_t).$$

Set x^* to be the smallest $x > 0$ satisfying equation (3.12). If $\phi_t < x^*$ then $d(t; 0) < x^*$ and $\phi_{t+1} < \phi_t$. This establishes that ϕ_t is a decreasing sequence and hence the limit of this sequence as $t \rightarrow \infty$ exists. Therefore, for any $\epsilon > 0$, there exists a T such that for all $t \geq T$,

$$-\epsilon < \phi_{t+1} - \phi_t \leq d(t; 0) \left(\frac{f(d(t; 0))}{d(t; 0)} \int_0^1 \frac{\lambda}{1-\lambda} \sigma(d\lambda) - 1 \right).$$

Since $\phi_t < x^*$ for all $t \geq 0$, $d(t; 0) < x^*$ for all $t \geq 0$. Therefore, from the definition of x^* , there exists a $C > 0$ such that

$$\frac{f(d(t; 0))}{d(t; 0)} \int_0^1 \frac{\lambda}{1-\lambda} \sigma(d\lambda) - 1 < -C.$$

It follows that for any $\epsilon > 0$, there exists a T such that for all $t \geq T$, $d(t; 0) \leq \epsilon/C$. As ϵ can be made arbitrarily small we have established that $\lim_{t \rightarrow \infty} d(t; 0) = 0$.

A.3. Proof of Theorem 3.2. The proof of this theorem for $R'_\sigma(\psi) < 1$ follows the same arguments as in the proof of case (i) of Theorem 2.3 in [15].

Assume now that $R'_\sigma(\psi) > 1$. Let σ_m be a sequence of distributions converging weakly to σ such that $\sigma_m < \sigma$ for all m . From this, we can state that for every m , $R_{\sigma_m}(\psi)$ is a continuous function and $R_{\sigma_m}(\psi) < R_\sigma(\psi)$ for all $\psi \in (0, 1]$. Furthermore, $R_{\sigma_m}(\psi) \rightarrow R_\sigma(\psi)$ for every $\psi \in [0, 1]$. These properties imply that, for m sufficiently large, there exists at least one solution to $\psi = R_{\sigma_m}(\psi)$ which is greater than ψ^* . Define

$$\tilde{\psi}_m := \inf \{ \psi : \psi = R_{\sigma_m}(\psi) \text{ and } \psi > \psi^* \}.$$

As $R_{\sigma_m}(\psi)$ is continuous, $\tilde{\psi}_m = R_{\sigma_m}(\tilde{\psi}_m)$. So $\tilde{\psi}_m$ is the ‘minimal’ solution to $\psi = R_{\sigma_m}(\psi)$ greater than ψ^* . Finally note that $\tilde{\psi}_m > \psi^*$. If this were not true, that is if $\psi^* = \tilde{\psi}_m$, then

$$R_{\sigma}(\psi^*) = \psi^* = \tilde{\psi}_m = R_{\sigma_m}(\tilde{\psi}_m) = R_{\sigma_m}(\psi^*),$$

which is a contradiction since $R_{\sigma_m}(\psi) < R_{\sigma}(\psi)$ for all $\psi \in (0, 1]$. We also note that since $R_{\sigma_m}(\psi) \rightarrow R_{\sigma}(\psi)$ for every $\psi \in [0, 1]$ it follows that $\tilde{\psi}_m \rightarrow \psi^*$ as $m \rightarrow \infty$. Now define

$$d_m(k) = \int_0^1 \frac{f(\tilde{\psi}_m)\lambda^{k+1}}{1 - \lambda + \lambda f(\tilde{\psi}_m)} \sigma_m(d\lambda), \quad \text{and} \quad d(0; k) = \int_0^1 \frac{f(\tilde{\psi}_m)\lambda^{k+1}}{1 - \lambda + \lambda f(\tilde{\psi}_m)} \sigma(d\lambda).$$

As $\tilde{\psi}_m \rightarrow \psi^*$, we can make $d(0; k)$ arbitrarily close to the equilibrium point corresponding to ψ^* by taking m sufficiently large. For all $k \geq 0$, $d_m(k) \leq d(0; k)$. We now show that $d_m(k) \leq d(t; k)$ for all $t \geq 0$ and all $k \geq 0$ by induction. Suppose that $d_m(k) \leq d(T; k)$ for all $k \geq 0$ and for some $T \geq 0$. Let $\bar{s}_k^{(m)}$ denote the moments of σ_m . As $d_m(k)$ is a solution to (2.6) with $\bar{s}_k^{(m)}$ replacing \bar{s}_k ,

$$\begin{aligned} d_m(k) &= (1 - f(d_m(0))) d_m(k+1) + f(d_m(0)) \bar{s}_{k+1}^{(m)} \\ &\leq (1 - f(d_m(0))) d_m(k+1) + f(d_m(0)) \bar{s}_{k+1} \\ &\leq (1 - f(d_m(0))) d(T; k+1) + f(d_m(0)) \bar{s}_{k+1} \\ &\leq (1 - f(d(T; 0))) d(T; k+1) + f(d(T; 0)) \bar{s}_{k+1} = d(T+1; k). \end{aligned}$$

Since $d_m(k) \leq d(t; k)$ for all $t \geq 0$ and all $k \geq 0$, it follows that $\liminf_{t \rightarrow \infty} d(t; 0) \geq \psi_m^* > \psi^*$. Hence, this is an unstable equilibrium point.

REFERENCES

- [1] Amarasekare, P. (1998) Allee effects in metapopulation dynamics. *The American Naturalist*, 152, 298-302.
- [2] Billingsley, P. (1999) *Convergence of probability measures*. 2nd Edition, Wiley, 1999.
- [3] Buckley, F.M. and Pollett, P.K. (2010) Limit theorems for discrete-time metapopulation models. *Probability Surveys*, 7, 53-83.
- [4] Courchamp, F., Berec, L. and Gascoigne, J. (2008) *Allee effects in ecology and conservation*. Oxford University Press.
- [5] Darling, R.W.R. and Norris, J.R. (2008) Differential equation approximations for Markov chains. *Probability Surveys*, 5, 37-79.

- [6] Gyllenberg, M. and Hanski, I. (1997) Habitat deterioration, habitat destruction, and metapopulation persistence in a heterogeneous landscape. *Theoretical Population Biology*, 52, 198-215.
- [7] Hall, L. S. , Krausman, P. R. and Morrison, M. L. (1997) The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin*, 25, 173-182.
- [8] Hanski, I. (1994) A practical model of metapopulation dynamics. *Journal of Animal Ecology*, 63, 151-162.
- [9] Hanski, I. and Gyllenberg, M. (1997) Uniting two general patterns in the distribution of species. *Science*, 275, 397-400.
- [10] Hanski, I., Moilanen, A., Pakkala, T. and Kuussaari, M. (1996) The quantitative incidence function model and persistence of an endangered butterfly metapopulation. *Conservation Biology*, 10, 578-590.
- [11] Hanski, I. and Ovaskainen, O. (2003) Metapopulation theory for fragmented landscapes. *Theoretical Population Biology*, 64, 119-127.
- [12] Hill, M.F. and Caswell, H. (2001) The effects of habitat destruction in finite landscapes: A chain-binomial metapopulation model. *Oikos*, 93, 321-331.
- [13] Hui, C. and Li, Z. (2003) Dynamical complexity and metapopulation persistence. *Ecological Modelling*, 164, 201-209.
- [14] Moilanen, A. (2004) SPOMSIM: software for stochastic patch occupancy models of metapopulation dynamics. *Ecological Modelling*, 179, 533-550.
- [15] McVinish, R. and Pollett, P.K. (2010) Limits of large metapopulations with patch-dependent extinction probabilities, *Advances in Applied Probability*, 42, 1172-1186.
- [16] McVinish, R. and Pollett, P.K. (2012) Central limit theorem for a discrete-time SIS model with individual variation, *Journal of Applied Probability*, to appear.
- [17] Mortelitti, A., Amori, G. and Boitani, L. (2010) The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. *Oecologia*, 163, 535-547.
- [18] Müller, A. and Stoyan, D. (2003) *Comparison methods for stochastic models and risks*, Wiley.
- [19] Ovaskainen, O. and Hanski, I. (2001) Spatially structured metapopulation models: Glocal and local assessment of metapopulation capacity. *Theoretical Population Biology*, 60, 281-302.

- [20] van der Meijden, E. and van der Veen-van Wijk, C.A.M. (1997) Tritrophic metapopulation dynamics. In I. Hanski and M.E. Gilpin (Eds.), *Metapopulation Biology: ecology, genetics and evolution*, Academic Press.
- [21] Widder, D.V. (1941) *The Laplace Transform*, Princeton University Press.
- [22] Zhou, S.-R., Lui, C.-Z. and Wang, G. (2004) The competitive dynamics of metapopulation subject to the Allee-like effect. *Theoretical Population Biology*, 65, 29-37.