A METAPOPULATION MODEL WITH LOCAL EXTINCTION PROBABILITIES THAT EVOLVE OVER TIME

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ABSTRACT. We study a variant of Hanski’s incidence function model that accounts for the evolution over time of landscape characteristics which affect the persistence of local populations. In particular, we allow the probability of local extinction to evolve according to a Markov chain. This covers the widely studied case where patches are classified as being either suitable or unsuitable for occupancy. Threshold conditions for persistence of the population are obtained using an approximating deterministic model that is realized in the limit as the number of patches becomes large.

1. INTRODUCTION

A metapopulation is a collection of local populations of a single species occupying spatially distinct habitat patches. This division of the population may be due to natural variation in the landscape or artificial fragmentation of the habitat. Although the local populations are geographically separated, they still interact through colonising patches that no longer support a local population. This process enables the species to persist despite local extinction events.

The aim of much of metapopulation ecology is to identify and quantify extinction risks. This is often achieved using Stochastic Patch Occupancy Models (SPOMs), which are well established in the ecology literature [13]. A SPOM is a discrete-time Markov chain that models the presence/absence of the focal species at each habitat patch in the metapopulation. The simplest example of a SPOM is the stochastic logistic model [37, 28], which provides a model of the number of occupied patches under very strong assumptions.

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Hanski [11] proposed a more realistic SPOM called the Incidence Function Model (IFM), which, since its inception, has been widely employed in empirical studies [30].

One of the most useful properties of the IFM is that the colonisation and extinction probabilities are parameterised in terms of landscape characteristics such as distance between patches and patch area. It is implicitly assumed that, when applying the IFM, the landscape is static. However, for many metapopulations, the dynamics of the landscape play an important role in the persistence/extinction of the species [34]. As an example, Hanski [12] mentions the marsh fritillary butterfly (Eurodryas aurinia) whose host plant (Succisa pratensis) occurs in forest clearings that are between two and ten years old. The metapopulation of sharp-tailed grouse (Tympanuchus phasianellus), which occupies areas of grassland, is similarly affected by landscape dynamics [2, 10]. For this species, fire opens new grassland areas and prevents the encroachment of forests. Other examples include metapopulations of the perennial herb (Polygonella basiramia) [5] and metapopulations of the beetle (Stephanopachys linearis), which breeds only in burned trees [32]. In these examples, the landscape dynamics are driven by secondary succession, and this is often the case regardless of whether the focal species depends on a seral community or the climax community.

There have been a number of approaches proposed to model metapopulations in dynamic landscapes. Several authors [18, 33, 38, 39] have incorporated habitat dynamics into the stochastic logistic model by allowing each patch to alternate between being suitable or unsuitable for supporting a local population according to some Markov chain [see also the related approach in 7]. Others [35, 16] have attempted to deal with landscape dynamics by incorporating the time elapsed since a patch was colonised. A third approach is to model the evolution of the relevant characteristics of the landscape and use these in the colonisation and extinction probabilities of the metapopulation model [12]. In this paper, we adopt this third approach.

Starting with a variant of the IFM, we model the landscape dynamics by allowing the probability of local extinction to evolve according to a continuous-state Markov chain. By modelling the landscape dynamics in this way, the approach of classifying patches as being suitable or unsuitable is included as a special case. Our aim is to derive threshold conditions for metapopulations with dynamic landscapes comparable to those available in the static landscape case [for example, 29]. To this end, a ‘law of large numbers’ is
derived which shows that the stochastic model can be well approximated by a certain deterministic model when the number of patches is large. This deterministic model is then used to derive the threshold condition. The work presented here builds on our previous analyses of metapopulations models \[21, 23, 26\]. All proofs are given in the Appendix.

2. Model description and main assumptions

As previously noted, the transition probabilities of the IFM \[11\] are determined by characteristics of the patches. For the \(i\)-th patch, these characteristics are its location \(z_i\), a weight \(a_i\) related to the size of the patch, and the probability \(s_i\) that a population occupying this patch survives a given period of time. For an \(n\)-patch metapopulation, its state at time \(t\) is described by the binary vector \(X^n_t = (X^n_{1,t}, \ldots, X^n_{n,t})\), where \(X^n_{i,t} = 1\) if patch \(i\) is occupied at time \(t\) and \(X^n_{i,t} = 0\) otherwise. Assuming a static landscape and conditional on the patch characteristics, the evolution of the metapopulation follows a discrete time Markov chain. It is assumed that the colonisation and extinction events occur in phases with observations of the state of the metapopulation made after the extinction phase. This type of phase structure has previously been used in \[1, 8, 14, 21, 23\]. Conditional on \(X^n_t\) and the patch characteristics, the \(X^n_{i,t+1}\) \((i = 1, \ldots, n)\) are independent with transitions given by

\[
P \left( X^n_{i,t+1} = 1 \mid X^n_t, z^n, a^n, s^n \right) = s_i X^n_{i,t} \left( n^{-1} \sum_{j=1}^{n} X^n_{j,t} D(z_i, z_j) a_j \right) \left( 1 - X^n_{i,t} \right), \tag{2.1} \]

where \(D(z, \tilde{z}) \geq 0\) is a measure of the ease of movement between patches located at \(z\) and \(\tilde{z}\), and \(f: [0, \infty) \mapsto [0, 1]\) (called the colonisation function). We note that although \(X_{i,t}\) appears in the colonisation probability for patch \(i\), it provides no contribution since patch \(i\) can only be colonised if \(X_{i,t} = 0\). Further explanation of this point can be found in McVinish and Pollett \[26\].

Although there are several ways in which landscape dynamics can be incorporated into the model defined by transition probabilities \(2.1\), we only consider the case where the local population survival probabilities evolve over time, but the patch areas and connectivity remain static. For each \(i\), let \(s_{i,t}\) denote the probability that the population occupying patch \(i\) survives from time \(t\) to time \(t + 1\). The transition probabilities for \(X^n_t\)
are now given by
\[
P(X_{i,t+1}^n = 1 \mid X_t^n, z^n, a^n, s^n_t) = s_{i,t}X_t^n + s_{i,t}f \left( n^{-1} \sum_{j=1}^n X_j^n D(z_i, z_j) a_j \right) (1 - X_{i,t}^n). \tag{2.2}
\]

Our analysis of the model (2.2) is based on a number of assumptions. The first four are essentially the same as those used in McVinish and Pollett [26].

(A) \(a_i \in (0, A]\) for some \(A < \infty\).

(B) \(z_i \in \Omega\) where \(\Omega\) is a compact subset of \(\mathbb{R}^d\).

(C) \(D(z, \tilde{z})\) defines a uniformly bounded and equicontinuous family of functions on \(\Omega\). That is, there exists a finite constant \(\bar{D}\) such that for all \(z_1, z_2 \in \Omega\), \(|D(z_1, z_2)| \leq \bar{D}\), and for every \(\epsilon > 0\) there exists a \(\delta > 0\) such that for all \(z_1, z_2\) with \(\|z_1 - z_2\| < \delta\)
\[
\sup_{z \in \Omega} |D(z_1, z) - D(z_2, z)| < \epsilon.
\]
Furthermore, \(D(z, \tilde{z}) > 0\) for all \((z, \tilde{z}) \in \Omega \times \Omega\).

(D) The colonisation function \(f\) is an increasing Lipschitz continuous function such that \(f(0) = 0\) and \(f'(0) > 0\).

Assumptions (A) and (B) are technical assumptions. Assumptions (C) and (D) are satisfied by most common choices of these functions. For example, it is usual to take \(D(z, \tilde{z})\) to be some function of the Euclidean distance between the two patches such as \(\exp(-\|z - \tilde{z}\|)\). A typical choice for the colonisation function is \(f(x) = 1 - \exp(-\beta x)\) for some \(\beta > 0\).

The next assumption concerns the landscape dynamics.

(E) For each \(i\), \(\{s_{i,t}\}_{t=0}^{\infty}\) is a Markov chain on \([0, 1]\) with transition kernel \(P(s, dr)\) common for all \(i\), and for \(i \neq j\), \(\{s_{i,t}\}_{t=0}^{\infty}\) and \(\{s_{j,t}\}_{t=0}^{\infty}\) are independent. The transition kernel is assumed to satisfy the weak Feller property, that is, for every continuous function \(h\) on \([0, 1]\), the function defined by
\[
Ph(s) := \int h(r)P(s, dr), \quad s \in [0, 1],
\]
is also continuous [27, Proposition 6.1.1(i)].

Although the assumption that the patches evolve independently has been previously used in metapopulation models with dynamic landscapes [18, 33, 38, 39], sometimes only implicitly, it must be noted that independence excludes some important forms of landscape
dynamic. In particular, disturbances that affect multiple patches instantaneously, such as widespread fires or droughts, are excluded by this assumption. The Markov chain model for the survival probabilities can incorporate the suitable/unsuitable approach to landscape dynamics. Patches that are unsuitable at time $t$ are equated with those patches for which $s_{i,t} = 0$; for any patch that is colonised with $s_{i,t} = 0$, the local population immediately goes extinct. Suitable patches are those for which $s_{i,t} > 0$. To recover the type of dynamic typically used, the Markov chain for the survival probabilities reduces to a Markov chain with two states $0$ and $s^*$; the transition kernel is given by

$$\begin{align*}
P(0, dr) &= p_0 \delta(s^* - r)dr + (1 - p_0) \delta(r)dr, \\
P(s^*, dr) &= p_1 \delta(s^* - r)dr + (1 - p_1) \delta(r)dr,
\end{align*}$$

for some $p_0, p_1 > 0$. For $x \not\in \{0, s^*\}$, $P(x, dr)$ can be set to ensure the weak Feller property holds.

The last of our main assumptions concerns the initial variation in the landscape. Let $C^+([0,1] \times \Omega)$ denote the class of continuous functions $h : [0,1] \times \Omega \mapsto [0,\infty)$. By Assumption (B), $\Omega$ is compact, so every function in $C^+([0,1] \times \Omega)$ is bounded. Consider the array of random measures $\sigma_{n,t}$ defined by

$$\int h(s, z)\sigma_{n,t}(ds, dz) := n^{-1} \sum_{i=1}^{n} a_i h(s_{i,t}, z_i), \quad \text{for all } h \in C^+([0,1] \times \Omega).$$

The measure $\sigma_{n,t}$ describes the landscape of the $n$ patch metapopulation model at time $t$. It is purely atomic placing mass $n^{-1} a_i$ at the point determined by patch $i$'s location and its survival probability at time $t$. We assume that $\sigma_{n,0}$ satisfies the following:

(F) As $n \to \infty$, $\sigma_{n,0} \xrightarrow{d} \sigma_0$ for some non–random measure $\sigma_0$, that is [17, Theorem 16.16]

$$\int h(s, z)\sigma_{n,0}(ds, dz) \xrightarrow{d} \int h(s, z)\sigma_0(ds, dz), \quad \text{for all } h \in C^+([0,1] \times \Omega).$$

Assumption (F) is satisfied if, for example, the random vectors $(z_i, a_i, s_{i,0})$ are independent and identically distributed. Although this assumption only concerns the initial variation in the landscape, it implies a similar ‘law of large numbers’ for the landscape at all subsequent times.
Lemma 2.1. Suppose Assumptions (A), (B), (E) and (F) hold. Then \( \sigma_{n,t} \xrightarrow{d} \sigma_t \), where \( \sigma_t \) is defined by the recursion
\[
\int h(s, z) \sigma_{t+1}(ds, dz) = \int h(s, z) \int P(r, ds) \sigma_t(dr, dz),
\]
for all \( h \in C^+([0, 1] \times \Omega) \).

3. Law of large numbers

Consider the array of random measures \( \mu_{n,t} \) constructed from the Markov chain \( X^n_t \) by
\[
\int h(s, z) \mu_{n,t}(ds, dz) := n^{-1} \sum_{i=1}^{n} a_i X^n_{i,t} h(s_{i,t}, z_i), \quad \text{for all } h \in C^+([0, 1] \times \Omega).
\]
The measure \( \mu_{n,t} \) has a similar structure to \( \sigma_{n,t} \), but only involves those patches that are occupied at time \( t \). These measures can be used to determine quantities such as the proportion of occupied patches in a given area weighted by the patch size. The following theorem describes the behaviour of the metapopulation as the number of patches tends to infinity.

Theorem 3.1. Suppose that Assumptions (A) – (F) hold and that \( \mu_{n,0} \xrightarrow{d} \mu_0 \) for some non–random measure \( \mu_0 \). Then \( \mu_{n,t} \xrightarrow{d} \mu_t \) for all \( t = 0, 1, \ldots \), where \( \mu_t \) is defined by the recursion
\[
\int h(s, z) \mu_{t+1}(ds, dz) = \int s \left\{ \int h(r, z) P(s, dr) \right\} \mu_t(ds, dz)
+ \int \left\{ \int h(r, z) P(s, dr) \right\} s f \left( \int D(z, \tilde{z}) \mu_t(d\tilde{s}, d\tilde{z}) \right) \sigma_t(ds, dz)
- \int \left\{ \int h(r, z) P(s, dr) \right\} s f \left( \int D(z, \tilde{z}) \mu_t(d\tilde{s}, d\tilde{z}) \right) \mu_t(ds, dz),
\]
for all \( h \in C^+([0, 1] \times \Omega) \).

For Theorem 3.1 to provide useful information on the evolution of the metapopulation, it is necessary that the limiting proportion of occupied patches is positive. If only a finite number of patches are initially occupied, then as \( n \to \infty \), the \( \mu_{n,0} \) will converge to the null measure, and, since \( f(0) = 0 \), it will follow that \( \mu_t \) is the null measure for all \( t \geq 0 \). A different type of analysis is required to analyse the evolution of the metapopulation.
when it is very close to extinction [Section 4 of 26 provides an example of this type of analysis with a static landscape].

A consequence of Theorem 3.1 is that the occupancy status of a single patch converges to a Markov chain with time dependent transition probabilities.

**Corollary 3.2.** Assume the conditions of Theorem 3.1 hold. For any $i$, if $X_{i,0} \xrightarrow{P} X_{i,0}$, then $X_{i,t}^{n} \xrightarrow{P} X_{i,t}$ for all $t \geq 0$, where

$$P(X_{i,t+1} = 1 \mid X_{i,t}, z_{i}, s_{i,t}) = s_{i,t}X_{i,t} + s_{i,t}f\left(\int D(z_{i}, z)\mu_{t}(ds, dz)\right)(1 - X_{i,t}). \quad (3.4)$$

The proof of Corollary 3.2 uses the same arguments as in the proof of Corollary 1 of McVinish and Pollett [23].

We may simplify recursion (3.3) by simplifying the evolution of the landscape. This is done by assuming that the landscape is in an equilibrium.

(G) For all $t \geq 0$, $\sigma_{t} = \sigma$ for some measure $\sigma$.

For some landscape dynamics, $\sigma_{t}$ will converge to an invariant measure. If the landscape has existed for a long time, then Assumption (G) should be reasonable.

**Lemma 3.3.** Suppose that the Markov chain with transition kernel $P$ is positive Harris and aperiodic. Then $\lim_{t \to \infty} \sigma_{t} = \sigma$, for some measure $\sigma$. Furthermore, $\sigma$ is a product measure.

Applying the same arguments as in McVinish and Pollett [24, Lemma 5], it can be shown that, for all $t \geq 0$, $\mu_{t}$ is absolutely continuous with respect to $\sigma$. Therefore, one might hope to obtain a recursion for the Radon-Nikodym derivative of $\mu_{t}$ with respect to $\sigma$. Define the measure $\nu$ such that, for any measurable subset $A$ of $[0, 1]$, $\nu(A) := \sigma(A \times \Omega)$. From Lemma 2.1, $\nu$ is an invariant measure for $P$. Assuming that the transition kernel $P$ is reversible with respect to $\nu$, it is possible interchange to the order of integration in (3.3) to obtain a recursion for the Radon-Nikodym derivative. However, this assumption can be avoided by using the dual kernel of the Markov chain. The dual kernel has been used by various authors studying Markov chains and processes [see 4, and references therein]. As we have been unable to find anything in the literature dealing explicitly with the case of interest here, we state the definition of the dual kernel and some basic results. In the following, $(S, \Sigma)$ denotes a general measure space.
Definition 3.1. Let $P$ be a sub-transition kernel on $(S, \Sigma)$ and let $\pi$ be a $\sigma$-finite measure on $(S, \Sigma)$. If there exists a sub-transition kernel $P^*$ such that
\[
\int_A \pi(dx) P(x, B) = \int_B \pi(dx) P^*(x, A),
\]for all $A, B \in \Sigma$, then $P^*$ is called a dual of $P$ with respect to $\pi$. If
\[
\int_A \pi(dx) P(x, B) = \int_B \pi(dx) P(x, A),
\]for all $A, B \in \Sigma$, then $P$ is said to be reversible with respect to $\pi$.

Remark. We shall see later that if $\pi$ is a subinvariant measure for $P$, then the dual of $P$ with respect to $\pi$ is determined uniquely $\pi$-almost everywhere, in that, for all $A \in \Sigma$, $P^*(x, A)$ is the same for $\pi$-almost all $x \in S$.

Notice (setting $B$ equal to $S$ in (3.6)) that if $P$ is reversible with respect to $\pi$, then $\pi$ is an invariant measure for $P$. More generally, we have the following.

Theorem 3.4. Let $P$ be a sub-transition kernel on $(S, \Sigma)$ and let $\pi$ be a $\sigma$-finite measure on $(S, \Sigma)$. Then $\pi$ is a subinvariant measure for $P$ if and only if there exists a dual $P^*$ for $P$ with respect to $\pi$. Further, $\pi$ is an invariant measure for $P$ if and only if $P^*$ is a transition kernel. If $P^*$ is dual for $P$, then $\pi$ is invariant for $P^*$ if and only if $P$ is a transition kernel.

Corollary 3.5. Let $\phi$ and $\psi$ be $\Sigma$-measurable functions. Then, under the conditions of Theorem 3.4, the dual $P^*$ satisfies
\[
\int \pi(dx) \phi(x) \int P(x, dy) \psi(y) = \int \pi(dx) \psi(x) \int P^*(x, dy) \phi(y).
\]
To apply the dual kernel, it is necessary to construct a Markov chain on $[0, 1] \times \Omega$. Define the transition kernel $Q$ such that for any measurable subset $A$ of $[0, 1] \times \Omega$, $Q((s, z), A) := \int P(s, A_z) \, \pi(dx)$ where $A_z = \{ s : (s, z) \in A \}$. The resulting Markov chain may be interpreted as $(s_t, z) \to (s_{t+1}, z)$ where $s_t$ is the Markov chain with transition kernel $P$. Applying Lemma 2.1 and Assumption (G), $\sigma$ is an invariant measure of $Q$. The dual kernel of $Q$ with respect to $\sigma$ is given by $Q^*((s, z), A) = P^*(s, A_z)$, where $P^*$ is the dual kernel of $P$ with respect to $\nu$. The integrals on the right-hand side of recursion (3.3) can be...
re-written as
\[
\int s \left\{ \int h(y, z)P(s, dr) \right\} \mu_t(ds, dz) = \int h(s, z) \left\{ \int r \frac{\partial \mu_t}{\partial \sigma}(r, z)P^*(s, dr) \right\} \sigma(ds, dz),
\]
\[
\int \left\{ \int h(r, z)P(s, dr) \right\} s f \left( \int D(z, \tilde{z})\mu_t(d\tilde{s}, d\tilde{z}) \right) \mu_t(ds, dz)
= \int h(s, z) f \left( \int D(z, \tilde{z})\mu_t(d\tilde{s}, d\tilde{z}) \right) \left\{ \int r \frac{\partial \mu_t}{\partial \sigma}(r, z)P^*(s, dr) \right\} \sigma(ds, dz),
\]
and
\[
\int \left\{ \int h(r, z)P(s, dr) \right\} s f \left( \int D(z, \tilde{z})\mu_t(d\tilde{s}, d\tilde{z}) \right) \sigma(ds, dz)
= \int h(s, z) \left\{ \int rP^*(s, dr) \right\} f \left( \int D(z, \tilde{z})\mu_t(d\tilde{s}, d\tilde{z}) \right) \sigma(ds, dz).
\]
Therefore, the Radon-Nikodym derivative of \( \mu_t \) with respect to \( \sigma \) satisfies the recursion
\[
\frac{\partial \mu_{t+1}}{\partial \sigma}(s, z) = \int r \frac{\partial \mu_t}{\partial \sigma}(r, z)P^*(s, dr) + f \left( \int D(z, \tilde{z})\mu_t(d\tilde{s}, d\tilde{z}) \right) \int \left( 1 - \frac{\partial \mu_t}{\partial \sigma}(r, z) \right) rP^*(s, dr).
\]
(3.7)

In addition to providing a simplified recursion for the measure \( \mu_t \), the Radon-Nikodym derivative has a nice interpretation as the probability of a given patch being occupied when the number of patches in the metapopulation is large.

**Corollary 3.6.** Suppose that Assumption (G) holds and let \((X_{i,t}, s_{i,t})\) be the Markov chain from Corollary 3.2. If
\[
\mathbb{P}(X_{i,0} = 1 \mid s_{i,0} = s, z_i = z) = \frac{\partial \mu_0}{\partial \sigma}(s, z),
\]
then
\[
\mathbb{P}(X_{i,t} = 1 \mid s_{i,t} = s, z_i = z) = \frac{\partial \mu_t}{\partial \sigma}(s, z),
\]
for all \( t \geq 0 \).
We would like to study the equilibrium behaviour of (3.3) recursion using the simpler recursion (3.7). To see why this is possible, let \( \mu_\infty \) be a stable fixed point of recursion (3.3), that is \( \mu_t \to \mu_\infty \) weakly as \( t \to \infty \). As the support of \( \sigma \) is compact by Assumption (B) and \( \frac{\partial \mu_t}{\partial \sigma} \) is bounded by one almost everywhere for all \( t \), we can show that \( \mu_\infty \) is absolutely continuous with respect to \( \sigma \) using a similar argument to McVinish and Pollett [24, Lemma 5]. Hence, the Radon-Nikodym derivative \( \frac{\partial \mu_\infty}{\partial \sigma} \) exists. Furthermore, by Scheffé’s lemma, if the sequence of densities \( \frac{\partial \mu_t}{\partial \sigma} \) given by recursion (3.7) converges almost everywhere as \( t \to \infty \), then this limit must be \( \frac{\partial \mu_\infty}{\partial \sigma} \). Therefore, the stable fixed points of the two recursions are equivalent.

The recursion (3.7) has some nice monotonicity properties which suggest the application of the powerful cone limit set trichotomy [15]. If it could be applied, then much of the difficulty in determining the threshold condition for the persistence of the metapopulation would be resolved as it would enable us to make very strong statements concerning the existence and stability of fixed points. Unfortunately, the operator defined by the right-hand side of (3.7) does not satisfy the necessary compactness property, so a slightly different approach is required. Our first step is to characterise the fixed points of recursion (3.7) in such a way that allows the cone limit set trichotomy to be used. This gives conditions for the existence and uniqueness of a non-zero fixed point. The stability of the fixed points is studied using a similar approach to [6].

Let \( \psi(z) = \int D(z, \tilde{z}) \mu_\infty(d\tilde{s}, d\tilde{z}) \). From recursion (3.7), the Radon-Nikodym derivative \( \frac{\partial \mu_\infty}{\partial \sigma} \) must satisfy

\[
\frac{\partial \mu_\infty}{\partial \sigma}(s, z) - (1 - f(\psi(z))) \int r \frac{\partial \mu_\infty}{\partial \sigma}(r, z) P^*(s, dr) = f(\psi(z)) \int r P^*(s, dr).
\]

(4.8)

Treating \( \psi \) as fixed, equation (4.8) is a Fredholm integral equation of the second kind. Let \( \mathcal{A} : C([0, 1] \times \Omega) \to C([0, 1] \times \Omega) \) be the operator \( \mathcal{A}g(s, z) = (1 - f(\psi(z))) \int g(r, z) r P^*(s, dr), \) \( g \in C([0, 1] \times \Omega) \). From Assumptions (C) and (D), if \( \mu_\infty \) is not the null measure, then
inf_{z \in \Omega} f(\psi(z)) > 0. Under these conditions, \( \|A\| \) is bounded:

\[
\|A\| = \sup_{\phi \in C([0,1] \times \Omega):\|\phi\| \leq 1} \left| \int g(r,z) r P^*(s,dr) \right| \\
\leq \sup_{\phi \in C([0,1] \times \Omega):\|\phi\| \leq 1} \sup_{s,z} (1 - f(\psi(z))) \|\phi\| \int r P^*(s,dr) \\
\leq 1 - \inf_{z \in \Omega} f(\psi(z)) < 1.
\]

Hence, \( A \) is a contraction and equation (4.8) has a unique solution given by the Neumann series [20, Theorem 2.9]

\[
\frac{\partial \mu_\infty}{\partial \sigma}(s,z) = \sum_{n=0}^{\infty} f(\psi(z))(1 - f(\psi(z)))^n \mathbb{E} \left( s_{n+1}^* \ldots s_1^* \mid s_0^* = s \right),
\]

where \( s_t^* \) is the Markov chain with transition kernel \( P^* \). As \( \psi(z) = \int D(z, \tilde{z}) \mu_\infty(d\tilde{s}, d\tilde{z}) \),

\[
\psi(z) = \int D(z, \tilde{z}) \sum_{n=0}^{\infty} f(\psi(\tilde{z}))(1 - f(\psi(\tilde{z})))^n \mathbb{E} \left( s_{n+1}^* \ldots s_1^* \mid s_0^* = s \right) \sigma(ds, d\tilde{z}). \tag{4.9}
\]

Using the cone limit set trichotomy, it can be shown that equation (4.9) has at most one non-zero solution under some additional assumptions. These are:

(H) The function \( f \) is strictly concave.

(I) For every \( z \in \Omega \) and every open neighbourhood \( N_z \) of \( z \), \( \sigma([0,1] \times N_z) > 0 \).

(J) For the dual process \( s_t^* \), \( \inf_{s} \mathbb{E}(s^*_i \mid s^*_0 = s) > 0 \).

Assumption (H) essentially excludes the possibility of an Allee-like effect in the metapopulation (see for example [25]). However, the assumption is sufficiently weak to allow a wide range of colonization functions. Assumption (I) is a technical assumption. If it does not hold, then \( \Omega \) is larger than the support of \( \sigma \). Finally, Assumption (J) is a relatively mild technical assumption. If the process of survival probabilities is reversible, then Assumption (J) implies that for some \( \epsilon > 0 \), \( P([\epsilon, 1], s) > 0 \). This excludes the possibility of moving to a small neighbourhood of 0 with high probability. If the process of survival probabilities takes only a discrete set of values \( \{s_1, s_2, \ldots \} \), then Assumption (J) holds if

\[
P(\{s_i \} \mid s_j) \geq c \nu(\{s_i \}),
\]

for all \( i, j \) and some \( c > 0 \). We now give our threshold condition for the persistence of a metapopulation in a dynamic landscape.
Theorem 4.1. Suppose Assumptions (A)-(D), (H)-(J) hold. Let $\mathcal{G} : C(\Omega) \mapsto C(\Omega)$ be the bounded linear operator

$$G\phi(z) := f'(0) \int D(z, \tilde{z}) \phi(\tilde{z}) \sum_{n=0}^{\infty} \mathbb{E} \left( s_{n+1}^* \ldots s_1^* \mid s_0^* = s \right) \sigma(ds, d\tilde{z}), \quad \phi \in C(\Omega),$$

and let $r(G)$ be the spectral radius of $G$. If $r(G) \leq 1$, then recursion (3.7) only has the trivial fixed point $\frac{\partial \mu}{\partial \sigma}(s, z) = 0$, and this fixed point is globally stable. If $r(G) > 1$, then recursion (3.7) has a unique non-zero fixed point and all non-zero trajectories converge to this fixed point.

Theorem 4.1 is an example of the kind of dichotomy observed in other metapopulation models not displaying an Allee-like effect such as Levins’ model. Without Assumption (H), the condition $r(G) > 1$ still implies the existence of a non-zero fixed point, but there may exist several non-zero fixed points in this case. On the other hand, if Assumption (H) is not imposed and $r(G) < 1$, then a non-zero fixed point may still exist.

5. Discussion

We have determined a threshold condition for the extinction/persistence of a metapopulation in a dynamic landscape. The applicability of our result hinges on the validity of the assumptions made in the analysis. While most are technical assumptions, satisfied by typical choices of parameters, the assumptions concerning the landscape dynamics will necessarily limit the range of metapopulations to which our result applies. In these concluding paragraphs, we discuss how these assumptions can potentially be relaxed and what tools will be needed for our work to be extended.

We have assumed that the only temporal variation in the landscape is due to the evolution of the local extinction probabilities at each patch; the patch areas and connectivity are assumed constant. It seems possible that variation in the patch areas could be incorporated into the model by allowing them to evolve following some Markov chain, and the analysis could be carried out using essentially the same arguments. On the other hand, allowing for temporal variation in the connectivity of patches, relevant to certain marine species [36], would require a different analysis and possibly involve techniques from the study of random graphs [9].

As previously noted, the independence assumption excludes from consideration certain forms of disturbance such as widespread fire and drought. A first step in weakening the
independence assumption would be to allow local spatial interaction in the landscape dynamics. For sufficiently weak spatial interactions, we would still expect a ‘law of large numbers’ result to be possible under appropriate technical assumptions. However, such weak spatial interaction is not going to provide a realistic model for widespread disturbances. As an extreme case of strong spatial interaction, suppose that for each time all patches had the same local extinction probability. In that case, we would expect any limiting process to still depend on the realization of the local extinction probability process. Tools from random dynamical systems \cite{3} may prove useful in the analysis of the limiting process in this case.

6. Proofs

6.1. Proof of Lemma 2.1. If \( \int h(s, z) \sigma_{n,t}(ds, dz) \xrightarrow{d} \int h(s, z) \sigma_t(ds, dz) \) for all \( h \in C^+([0, 1] \times \Omega) \), then \( \sigma_{n,t} \xrightarrow{d} \sigma_t \) \cite[Theorem 16.16]{17}. We use induction on \( t \) to prove weak convergence of the random measures \( \sigma_{n,t} \) to non–random measures \( \sigma_t \). By Assumption (F), \( \sigma_{n,0} \xrightarrow{d} \sigma_0 \) for some non–random measure \( \sigma_0 \). The conditional expectation of \( \int h(s, z) \sigma_{n,t+1}(ds, dz) \) given \( (s^n_t, a^n, z^n) \) is

\[
\mathbb{E} \left( \int h(s, z) \sigma_{n,t+1}(ds, dz) \mid s^n_t, a^n, z^n \right) = n^{-1} \sum_{i=1}^{n} a_i \int h(\tilde{s}, z_i)P(s, d\tilde{s})
\]

\[
= \int \left\{ \int h(\tilde{s}, z)P(s, d\tilde{s}) \right\} \sigma_{n,t}(ds, dz).
\]

Suppose that \( \sigma_{n,t} \xrightarrow{d} \sigma_t \) for some non–random measure \( \sigma_t \). If \( \int h(\tilde{s}, z)P(s, d\tilde{s}) \in C^+([0, 1] \times \Omega) \), then

\[
\lim_{n \to \infty} \mathbb{E} \left( \int h(s, z) \sigma_{n,t+1}(ds, dz) \mid s^n_t, a^n, z^n \right) = \int \left\{ \int h(\tilde{s}, z)P(s, d\tilde{s}) \right\} \sigma_t(d\tilde{s}, dz).
\]

Take \( (s, z) \to (s', z') \). Then

\[
\lim_{(s, z) \to (s', z')} \int h(r, z)P(s, dr) = \lim_{s \to s'} \int h(r, z')P(s, dr) + \lim_{(s, z) \to (s', z')} \int [h(r, z) - h(r, z')] P(s, dr).
\]

From Assumption (E), \( P \) has the weak Feller property, so \( \int h(r, z')P(s, dr) \to \int h(r, z')P(s', dr) \) as \( s \to s' \). Now

\[
\left| \lim_{(s, z) \to (s', z')} \int [h(r, z) - h(r, z')] P(s, dr) \right| \leq \sup_{s \in [0, 1]} |h(s, z) - h(s, z')|.
\]
Since $[0, 1] \times \Omega$ is compact, the Heine-Cantor Theorem implies that $h$ is uniformly continuous. Therefore, \( \int h(r, z)P(s, dr) \to \int h(r, z')P(s, dr) \) as $z \to z'$, uniformly in $s$. Hence, \( \int h(r, z)P(s, dr) \in C^+([0, 1] \times \Omega) \).

The conditional variance of \( \int h(s, z)\sigma_{n,t+1}(ds, dz) \) can be bounded by
\[
\text{var} \left( \int h(s, z)\sigma_{n,t+1}(ds, dz) \mid s^n_t, a^n, z^n \right) \leq n^{-1} A^2 \sup_{(s, z) \in [0,1] \times \Omega} |h(s, z)|^2.
\]

As the conditional variance goes to zero in probability, we can apply a Chebyshev type inequality [22] Appendix C] to conclude that
\[
\int h(s, z)\sigma_{n,t+1}(ds, dz) \overset{p}{\to} \int \left\{ \int h(s, z)P(s, ds) \right\} \sigma_t(ds, dz).
\]
\[
= \int h(s, z) \left\{ \int P(s, ds) \sigma_t(ds, dz) \right\}.
\]
\[
= \int h(s, z)\sigma_{t+1}(ds, dz).
\]

Hence, $\sigma_{n,t+1} \overset{d}{\to} \sigma_{t+1}$. The recursion for $\sigma_{t+1}$ is determined by equation (6.10).

6.2. Proof of Theorem 3.1 The proof follows closely the arguments of the proof of Lemma [21] and the proof of Theorem 3.1 [26]. We again use that fact that if $\int h \, dm_n \overset{d}{\to} \int h \, d\mu$ for all $h \in C^+([0, 1] \times \Omega)$ then $m_n \overset{d}{\to} \mu$ [17, Theorem 16.16] and apply mathematical induction on $t$ to prove weak convergence of the random measures $m_{n,t}$ to non–random measures $\mu_t$. By assumption $\mu_{n,0} \overset{d}{\to} \mu_0$ for some non–random measure $\mu_0$. Suppose that $\mu_{n,t} \overset{d}{\to} \mu_t$ for some non–random measure $\mu_t$. Then
\[
\mathbb{E} \left( \int h \, dm_{n,t+1} \mid X^n_t, s^n_t, a^n, z^n \right) = n^{-1} \sum_{i=1}^n a_i \mathbb{E} \left( h(s_{i,t+1}, z_i) \mid s_{i,t}, z_i \right) \mathbb{E} \left( X^n_{i,t+1} \mid X^n_t, s^n_t, a^n, z^n \right)
\]
\[
= \int s \left\{ \int h(r, z)P(s, dr) \right\} \mu_{n,t}(ds, dz)
\]
\[
+ \int s \left\{ \int h(r, z)P(s, dr) \right\} f \left( \int D(z, \tilde{z}) \mu_t(d\tilde{s}, d\tilde{z}) \right) \sigma_{n,t}(ds, dz)
\]
\[
- \int s \left\{ \int h(r, z)P(s, dr) \right\} f \left( \int D(z, \tilde{z}) \mu_t(d\tilde{s}, d\tilde{z}) \right) \mu_{n,t}(ds, dz) + \epsilon_{n,t}(h),
\]
where
\[
|\epsilon_{n,t}(h)| \leq C \left( \int \int h(r, z)P(s, dr)\sigma_n(ds, dz) \right) \sup_{z \in \Omega} \left| \int D(z, \tilde{z}) \mu_{n,t}(d\tilde{s}, d\tilde{z}) - \int D(z, \tilde{z}) \mu_t(d\tilde{s}, d\tilde{z}) \right|,
\]
for some constant $C > 0$ as $f$ is Lipschitz continuous. Applying a small modification of Theorem 3.1 of [31] and Assumption $(C)$, it follows that if $\mu_{n,t} \overset{d}{\to} \mu_t$, a non-random measure, then

$$\sup_{z \in \Omega} \left| \int D(z, \tilde{z})\mu_{n,t}(d\tilde{s}, d\tilde{z}) - \int D(z, \tilde{z})\mu_t(d\tilde{s}, d\tilde{z}) \right| \to 0.$$

We need both $s \int h(r, z)P(s, dr)$ and $s \int h(r, z)P(s, dr)f(\int D(z, \tilde{z})\mu_t(d\tilde{s}, d\tilde{z}))$ to be in $C^+([0, 1] \times \Omega)$. By Assumption $(C)$, $f(\int D(z, \tilde{z})\mu_t(d\tilde{s}, d\tilde{z})) \in C^+([0, 1] \times \Omega)$, and it has been shown in the proof of Lemma 2.1 that $\int h(r, z)P(s, dr) \in C^+([0, 1] \times \Omega)$. Therefore, both of the required functions are in $C^+([0, 1] \times \Omega)$. By the induction hypothesis, $\mu_{n,t} \overset{d}{\to} \mu_t$ for some non-random measure $\mu_t$. Therefore,

$$E \left( \int h \, d\mu_{n,t+1} \mid X^n_t, s^n_t, a^n_t, z^n_t \right) \overset{P}{\to} \int s \left\{ \int h(r, z)P(s, dr) \right\} \mu_t(ds, dz) + \int s \left\{ \int h(r, z)P(s, dr) \right\} f \left( \int D(z, \tilde{z})\mu_t(d\tilde{s}, d\tilde{z}) \right) \sigma_t(ds, dz) - \int s \left\{ \int h(r, z)P(s, dr) \right\} f \left( \int D(z, \tilde{z})\mu_t(d\tilde{s}, d\tilde{z}) \right) \mu_t(ds, dz).$$

The conditional variance of $\int h(s, z)\mu_{n,t+1}(ds, dz)$ can be bounded by $n^{-1}A^2\sup |h(s, z)|^2$. Applying a Chebyshev type inequality [22, Appendix C], we conclude that $\int h \, d\mu_{n,t+1}$ converges to $\int h \, d\mu_{t+1}$ in probability, and hence in distribution.

6.3. **Proof of Lemma 3.3.** From Lemma 2.1 for any bounded continuous function $h$,

$$\int h(s, z)\sigma_t(ds, dz) = \int h(s, z) \int P^t(\tilde{s}, ds)\sigma_0(d\tilde{s}, dz),$$

where $P^t$ is the $t$-step transition kernel of the Markov chain. As the Markov chain is positive Harris and aperiodic, it has a unique invariant measure and, by Meyn and Tweedie [27, Theorem 13.3.3],

$$\int h(s, z)P^t(\tilde{s}, ds) \to \int h(s, z)\nu(ds),$$

for every $(\tilde{s}, z)$ as $t \to \infty$. By the dominated convergence theorem,

$$\int \int h(s, z)P^t(\tilde{s}, ds)\sigma_0(d\tilde{s}, dz) \to \int \left\{ \int h(s, z)\nu(ds) \right\} \sigma_0(d\tilde{s}, dz).$$

Now define the measure $\tilde{\sigma}_0$, such that for any measurable subset $A$ of $\Omega$, $\tilde{\sigma}_0(A) := \sigma_0([0, 1] \times A)$. Since $\int h(s, z)\nu(ds)$ does not depend on $\tilde{s}$,

$$\int \left\{ \int h(s, z)\nu(ds) \right\} \sigma_0(d\tilde{s}, dz) = \int h(s, z)\nu(ds)\tilde{\sigma}_0(dz).$$
Hence, $\sigma_t \to \nu \times \bar{\sigma}_0$.

6.4. Proof of Theorem 3.4. Let $P$ be a sub-transition kernel on $(S, \Sigma)$ and let $\pi$ be a $\sigma$-finite measure on $(S, \Sigma)$. We first show that if $\pi$ is a subinvariant measure for $P$, then there exists a sub-transition kernel $P^*$ satisfying Definition 3.1. Suppose $\pi$ is subinvariant for $P$. For $A \in \Sigma$, define

$$\eta_A(\cdot) := \int_A \pi(dx)P(x, \cdot).$$

It is a measure on $(S, \Sigma)$ because $P(x, \cdot)$ is a measure on $(S, \Sigma)$. It is also clear that $\eta_A$ is absolutely continuous with respect to $\pi$, because if $N \in \Sigma$ is any $\pi$-null set then

$$\eta_A(N) = \int_A \pi(dx)P(x, N) \leq \int_S \pi(dx)P(x, N) \leq \pi(N) = 0.$$ 

So, by the Radon-Nikodym theorem, there exists a function $P^*: S \times \Sigma \mapsto [0, \infty)$ such that $P^*(\cdot, A)$ is a $\Sigma$-measurable function, and for all $B \in \Sigma$,

$$\int_A \pi(dx)P(x, B) = \eta_A(B) = \int_B \pi(dx)P^*(x, A).$$

Hence, $P^*$ is determined uniquely $\pi$-almost everywhere by equation (3.5). It remains to show that, for $\pi$-almost all $x \in S$, $P^*(x, \cdot)$ is a measure on $(S, \Sigma)$ with $P^*(x, S) \leq 1$.

For any $A \in \Sigma$, $P^*(\cdot, A)$ is the Radon-Nikodym derivative of $\eta_A$ with respect to $\pi$. As $\eta_\emptyset$ is the null measure, $P^*(x, \emptyset) = 0$ for $\pi$-almost all $x \in S$. To show that $P^*(x, \cdot)$ is countably additive, let $\{B_k\}$ be a sequence of pairwise disjoint sets in $\Sigma$. We want to show that the Radon-Nikodym derivative of $\eta_{\cup_k B_k}$ with respect to $\pi$ is $\sum_k P^*(\cdot, B_k)$. For any $A \in \Sigma$,

$$\eta_{\cup_k B_k}(A) = \int_{\cup_k B_k} \pi(dx)P(x, A)$$

$$= \sum_k \int_{B_k} \pi(dx)P(x, A)$$

$$= \sum_k \int_A \pi(dx)P^*(x, B_k)$$

$$= \int_A \pi(dx) \sum_k P^*(x, B_k).$$

Hence, $P^*(x, \cup_k B_k) = \sum_k P^*(x, B_k)$ for $\pi$-almost all $x \in S$. Finally, since $\pi$ is subinvariant for $P$, we have, for any $A \in \Sigma$,

$$\int_A \pi(dx)P^*(x, S) = \int_S \pi(dx)P(x, A) \leq \pi(A).$$
Hence, by the Radon-Nikodym Theorem, $P^*(x, S) \leq 1$ for $\pi$-almost all $x \in S$.

We now show that if there exists a dual $P^*$ for $P$ with respect to $\pi$, then $\pi$ is subinvariant. Since $P^*$ is a sub-transition kernel, $P^*(x, S) \leq 1$ for all $x \in S$. On setting $B$ equal to $S$ in equation (3.5) we see that

$$\int_S \pi(dx) P(x, A) = \int_A \pi(dx) P^*(x, S) \leq \int_A \pi(dx) = \pi(A),$$

that is, $\pi$ is subinvariant for $P$. This completes the proof of the first part of Theorem 3.4.

To prove the second part we note that if $P^*$ is a transition kernel then $P^*(x, S) = 1$ for all $x \in S$. In that case, inequality (6.11) becomes equality, and $\pi$ is seen to be invariant.

On the other hand, if $\pi$ is invariant for $P$, then $\pi(A) = \int_S \pi(dx) P(x, A) = \int_A \pi(dx) P^*(x, S)$, for all $A \in \Sigma$. Therefore, $P^*(x, S) = 1$ for $\pi$-almost all $x \in S$, and $P^*$ is a transition kernel. The final part is proved in similar vein.

6.5. Proof of Corollary 3.5. Suppose the conditions of Theorem 3.4 hold, and $P^*$ is a sub-transition kernel that satisfies equation (3.5). Let $\phi$ and $\psi$ be the simple functions $\phi(x) = \sum_k a_k \mathbb{I}(x \in A_k)$ and $\psi(x) = \sum_k b_k \mathbb{I}(x \in B_k)$, where $a_k, b_k \in \mathbb{R}$ and $A_k, B_k$ are $\Sigma$-measurable sets. Then

$$\int \pi(dx) \phi(x) \int P(x, dy) \psi(y) = \int \pi(dx) \sum_k a_k \mathbb{I}(x \in A_k) \int P(x, dy) \sum_j b_j \mathbb{I}(y \in B_j)$$

$$= \sum_k \sum_j a_k b_j \int \pi(dx) \mathbb{I}(x \in A_k) \int P(x, dy) \mathbb{I}(y \in B_j)$$

$$= \sum_k \sum_j a_k b_j \int_{A_k} \pi(dx) P(x, B_j)$$

$$= \sum_k \sum_j a_k b_j \int_{B_j} \pi(dx) P^*(x, A_k)$$

$$= \int \pi(dx) \sum_j b_j \mathbb{I}(x \in B_j) \int P^*(x, dy) \sum_k a_k \mathbb{I}(y \in A_k)$$

$$= \int \pi(dx) \psi(x) \int P^*(x, dy) \phi(y).$$

The result holds for simple functions. Now let $\phi$ and $\psi$ be any $\Sigma$-measurable functions, then we can decompose them as $\phi = \phi^+ - \phi^-$ and $\psi = \psi^+ - \psi^-$, where $\phi^+, \phi^-, \psi^+, \psi^- \geq 0$ are $\Sigma$-measurable functions. Then there exists sequences of non-negative, non-decreasing...
simple functions \((\phi^+_n), (\phi^-_n), (\psi^+_n)\) and \((\psi^-_n)\) such that \(\phi^+_n \to \phi^+, \phi^-_n \to \phi^-, \psi^+_n \to \psi^+\) and \(\psi^-_n \to \psi^-\), with convergence interpreted pointwise. The result follows by applying the Monotone Convergence Theorem and linearity of integration.

6.6. **Proof of Corollary 3.6.** Although we will always be conditioning on the patch location, this will not be made explicit to simplify the expressions. We shall also drop the dependence on \(i\). Define \(\psi_t(z) = \int D(z, \hat{z}) \mu_t(d\hat{s}, d\hat{z})\). Then \((X_t, s_t)\) is a Markov chain on \([0,1] \times [0,1]\) with transition kernel

\[
\begin{align*}
P(X_{t+1} = 1, s_{t+1} \in A \mid X_t = x, s_t = s) &= (sx + sf(\psi_t(z))(1 - x)) \int_A P(s, dr) \\
P(X_{t+1} = 0, s_{t+1} \in A \mid X_t = x, s_t = s) &= ((1 - s)x + (1 - sf(\psi_t(z)))(1 - x)) \int_A P(s, dr),
\end{align*}
\]

for any measurable set \(A \subset [0,1]\). Note that \(s_t\) is itself a Markov chain on \([0,1]\) with transition kernel \(P(x, dy)\) and invariant distribution \(\nu\). Assume that, marginally, the Markov chain \(\{s_t\}\) is stationary. To compute the conditional probability \(P(X_t = 1 \mid s_t = s)\), note that

\[
P(X_{t+1} = 1, s_{t+1} \in A) = \int P(X_{t+1} = 1, s_{t+1} \in A \mid X_t = 1, s_t = s) P(X_t = 1 \mid s_t = s) \nu(ds)
\]

\[
+ \int P(X_{t+1} = 1, s_{t+1} \in A \mid X_t = 0, s_t = s) P(X_t = 0 \mid s_t = s) \nu(ds)
\]

\[
= \int \left\{ \int_A P(s, dr) \right\} s \nu(X_t = 1 \mid s_t = s) \nu(ds)
\]

\[
+ \int \left\{ \int_A P(s, dr) \right\} sf(\psi_t(z)) (1 - P(X_t = 1 \mid s_t = s)) \nu(ds). \tag{6.12}
\]

Using the dual kernel \(P^*\),

\[
\int \int 1(r \in A) P(s, dr) s \nu(X_t = 1 \mid s_t = s) \nu(ds)
\]

\[
= \int \left\{ \int P^*(s, dr) r \nu(X_t = 1 \mid s_t = r) \right\} 1(s \in A) \nu(ds) \tag{6.13}
\]

and

\[
\int \int 1(r \in A) P(s, dr) s (1 - P(X_t = 1 \mid s_t = s)) \nu(ds)
\]

\[
= \int \left\{ \int P^*(s, dr) (1 - P(X_t = 1 \mid s_t = r)) \right\} 1(s \in A) \nu(ds). \tag{6.14}
\]
Substituting (6.13) and (6.14) into equation (6.12) yields
\[ \mathbb{P}(X_{t+1} = 1, s_{t+1} \in A) = \int 1(s \in A)\mathbb{P}(X_{t+1} = 1 | s_{t+1} = s)\nu(ds) \]
\[ = \int \left\{ \int P^*(s, dr)\mathbb{P}(X_t = 1 | s_t = r) \right\} 1(s \in A)\nu(ds) \]
\[ + \int \left\{ \int \psi_t(z)\int P^*(s, dr)(1 - \mathbb{P}(X_t = 1 | s_t = r)) \right\} 1(s \in A)\nu(ds). \]

From the Radon-Nikodym theorem (uniqueness up to a \( \sigma \)-null set),
\[ \mathbb{P}(X_{t+1} = 1 | s_{t+1} = s) \]
\[ = \int r\mathbb{P}(X_t = 1 | s_t = r)P^*(s, dr) + \psi_t(z)\int (1 - \mathbb{P}(X_t = 1 | s_t = r))rP^*(s, dr). \]
Comparing with (3.7), we see that if
\[ \mathbb{P}(X_0 = 1 | s_0 = s) = \frac{\partial \mu_0}{\partial \sigma}(s, z), \]
then
\[ \mathbb{P}(X_t = 1 | s_t = s) = \frac{\partial \mu_t}{\partial \sigma}(s, z), \]
for all \( t \geq 0 \).

6.7. Proofs of Theorem 4.1. The first step in the proof is to express equation (4.9) in a form that facilitates the application of the cone limit set trichotomy. Let
\[ \alpha_m(s) = \mathbb{E}(s^*_{m+1} \ldots s^*_1 | s^*_0 = s) - \mathbb{E}(s^*_{m+2} \ldots s^*_1 | s^*_0 = s) \quad (\geq 0). \]
Then we may express equation (4.9) as
\[ \psi(z) = \int D(z, \tilde{z})\sum_{n=0}^{\infty} f(\psi(z))(1 - f(\psi(z)))^n\mathbb{E}(s^*_{n+1} \ldots s^*_1 | s^*_0 = s)\sigma(ds, d\tilde{z}) \]
\[ = \int D(z, \tilde{z})f(\psi(z))\sum_{n=0}^{\infty} (1 - f(\psi(z)))^n \left\{ \sum_{m=n}^{\infty} \alpha_m(s) \right\} \sigma(ds, d\tilde{z}) \]
\[ = \int D(z, \tilde{z})f(\psi(z))\sum_{m=0}^{\infty} \alpha_m(s) \sum_{m=0}^{\infty} (1 - f(\psi(z)))^n\sigma(ds, d\tilde{z}) \]
\[ = \int D(z, \tilde{z})\sum_{m=0}^{\infty} \alpha_m(s) \left( 1 - (1 - f(\psi(z)))^{m+1} \right) \sigma(ds, d\tilde{z}). \] (6.15)

Let \( \mathcal{H} : C(\Omega) \rightarrow C(\Omega) \) be the operator defined by the right-hand side of equation (6.15).
Let \( K \) denote the reproducing cone of non-negative functions on \( \Omega \) and let \( \bar{K} \) denote the interior of \( K \). The cone \( K \) is equipped with the partial ordering \( \phi_1 \leq \phi_2 \) if \( \phi_1(z) \leq \phi_2(z) \).
for all $z \in \Omega$. The cone limit set trichotomy can be applied if $\mathcal{H}$ has the following properties:

(i) continuity;
(ii) order compactness; for any $\chi_1, \chi_2 \in K$, $\mathcal{H}$ maps the set $\{ \phi : \chi_1 \leq \phi \leq \chi_2 \}$ to a relatively compact set.
(iii) monotonicity; if $\phi_1 \leq \phi_2$, then $\mathcal{H}\phi_1 \leq \mathcal{H}\phi_2$.
(iv) strong positivity; if $\phi \in K \setminus \{ 0 \}$, then $\mathcal{H}\phi \in \bar{K}$.
(v) strong sublinearity; if $\lambda \in (0, 1)$ and $\phi \in \bar{K}$, then $\mathcal{H}(\lambda \phi) - \lambda \mathcal{H}\phi \in \bar{K}$.

We now proceed to show these properties hold.

**(i) continuity:** The operator $\mathcal{H}$ is continuous if

$$\lim_{k \to \infty} \sup_{z \in \Omega} \left| \int D(z, \tilde{z}) \sum_{m=0}^{\infty} \alpha_m(s) \left[ \left[ 1 - (1 - f(\phi_k(\tilde{z})))^{m+1} \right] - \left[ 1 - (1 - f(\phi(\tilde{z})))^{m+1} \right] \right] \sigma(ds, d\tilde{z}) \right| = 0$$

for any sequence of functions $\phi_k \in C(\Omega)$ such that $\phi_k \to \phi$. If $\phi_k \to \phi$, then

$$\sum_{m=0}^{\infty} \alpha_m(s) \left[ 1 - (1 - f(\phi_k(z)))^{m+1} \right] \to \sum_{m=0}^{\infty} \alpha_m(s) \left[ 1 - (1 - f(\phi(z)))^{m+1} \right]$$

for each $(s, z) \in [0, 1] \times \Omega$. Since $D$ is uniformly bounded, continuity of $\mathcal{H}$ follows from the dominated convergence theorem.

**(ii) order compactness:** For any $\chi_1, \chi_2 \in K$, let $\phi_1, \phi_2, \ldots$ be a sequence of functions in $K$ such that $\chi_1 \leq \phi_i \leq \chi_2$ for all $i$. By the Arzelà-Ascoli theorem, if the sequence of functions $\mathcal{H}\phi_1, \mathcal{H}\phi_2, \ldots$ is uniformly bounded and equicontinuous, then $\mathcal{H}$ is order compact. The sequence is uniformly bounded as for any $\phi$,

$$\mathcal{H}\phi \leq \int D(z, \tilde{z}) \left\{ \sum_{m=0}^{\infty} \alpha_m(s) \right\} \sigma(ds, d\tilde{z}) \leq \bar{D} \int \sigma(ds, d\tilde{z}).$$

To show the sequence of functions is equicontinuous, note that for any $\phi \in C(\Omega)$ and $z_1, z_2 \in \Omega$,

$$|\mathcal{H}\phi(z_1) - \mathcal{H}\phi(z_2)| \leq \int |D(z_1, \tilde{z}) - D(z_2, \tilde{z})| \sigma(ds, d\tilde{z}).$$

As $D$ is equicontinuous, so is the sequence of functions $\mathcal{H}\phi_1, \mathcal{H}\phi_2, \ldots$ Therefore, $\mathcal{H}$ is order compact.
(iii) monotonicity: Suppose $\phi_1 \leq \phi_2$ in the partial ordering on $K$. Then, for any $z \in \Omega,$

$$\mathcal{H}\phi_2(z) - \mathcal{H}\phi_1(z)$$

$$= \int D(z, \tilde{z}) \sum_{m=0}^{\infty} \alpha_m(s) \left[ [1 - (1 - f(\phi_2(\tilde{z})))^{m+1}] - [1 - (1 - f(\phi_1(\tilde{z})))^{m+1}] \right] \sigma(ds, d\tilde{z}).$$

For any $m \geq 0$, $[1 - (1 - f(x))^{m+1}]$ is an increasing function of $x$. Therefore, $\mathcal{H}$ is a monotone operator.

(iv) strong positivity: For any $\phi \in K$ such that $\phi \neq 0$ and any $z \in \Omega,$

$$\mathcal{H}\phi(z) \geq \int D(z, \tilde{z})\mathbb{E}(s_i^* \mid s_0^* = s) f(\phi(\tilde{z}))\sigma(ds, d\tilde{z}).$$

By Assumption (I), $\sigma_0(N_z) > 0$ for every $z \in \Omega$ and neighbourhood $N_z$ of $z$. As $\phi \neq 0$, there is a $z \in \Omega$ and neighbourhood $N_z$ such that $\phi(\tilde{z}) > 0$ for all $\tilde{z} \in N_z$. By Assumption (J), $\inf_s \mathbb{E}(s_i^* \mid s_0^* = s) > 0$. Therefore, $\mathcal{H}\phi(z) > 0$ for all $z \in \Omega$.

(v) strongly sublinear: By Assumption (H), $f$ is concave, so $(1 - (1 - f(x))^m$ is also concave for $m = 1, 2, \ldots$. For any $\lambda \in (0, 1), \phi \in \hat{K}$ and $z \in \Omega,$

$$\mathcal{H}(\lambda \phi)(z) - \lambda \mathcal{H}\phi(z)$$

$$= \int D(z, \tilde{z}) \sum_{m=0}^{\infty} \alpha_m(s) \left[ [1 - (1 - f(\lambda \phi(\tilde{z})))^{m+1}] - \lambda [1 - (1 - f(\phi(\tilde{z})))^{m+1}] \right] \sigma(ds, d\tilde{z})$$

$$\geq \int D(z, \tilde{z}) [f(\lambda \phi(\tilde{z})) - \lambda f(\phi(\tilde{z}))] \alpha_0(s) \sigma(ds, d\tilde{z}).$$

By Assumption (D), for any $(z, \tilde{z}) \in \Omega \times \Omega, D(z, \tilde{z}) > 0$. Also, Assumption (H) implies that $f(\lambda x) - \lambda f(x) > 0$ for all $x > 0, \lambda \in (0, 1)$. Therefore, $\mathcal{H}(\lambda \phi) - \lambda \mathcal{H}\phi \in \hat{K}$ for any $\lambda \in (0, 1), \phi \in \hat{K}$. Hence, $\mathcal{H}$ is strongly sublinear.

The conditions of the cone limit set trichotomy are satisfied. Therefore, either (i) $\psi = 0$ is the only fixed point of $\mathcal{H}$, or (ii) $\mathcal{H}$ has a unique non-zero fixed point and this fixed point must be in $\hat{K}$, or (iii) for every $\phi \neq 0$, successive applications of the operator $\mathcal{H}$ leads to an unbounded sequence. In proving order compactness, we have shown that $\mathcal{H}$ is bounded. Therefore, (iii) is excluded as a possibility. We can conclude that $\mathcal{H}$ has at most one non-zero fixed point.

It can be shown that $\mathcal{H}\phi \leq G\phi$ for any $\phi \in K$ with equality if and only if $\phi = 0$. As in Lemmas A.1 and A.2 of McVinish and Pollett [26], the Krein-Rutman theorem [19] can
then be used to show \( \mathcal{H} \) has only the zero fixed point if \( r(\mathcal{H}) \leq 1 \) and it has a non-zero fixed point if \( r(\mathcal{H}) > 1 \).

It remains to determine the stability of the fixed points. Let \( \mathcal{M} \) be the set of non-negative functions on \([0, 1] \times \Omega\), integrable with respect to \( \sigma \) and bounded by one. The space \( \mathcal{M} \) can be equipped with the partial ordering \( \phi_1 \leq \phi_2 \) if \( \phi_1(s, z) \leq \phi_2(s, z) \), \( \sigma \)-almost everywhere. Define the operator \( \widetilde{\mathcal{H}} : \mathcal{M} \mapsto \mathcal{M} \) by the right-hand side of equation \[6.7\], that is, for any \( \phi \in \mathcal{M} \),

\[
\widetilde{\mathcal{H}} \phi(s, z) := \left(1 - f \left( \int D(z, \tilde{z}) \phi(\tilde{s}, \tilde{z}) \sigma(d\tilde{s}, d\tilde{z}) \right) \right) \int r \phi(r, z) P^*(s, dr) \\
+ f \left( \int D(z, \tilde{z}) \phi(\tilde{s}, \tilde{z}) \sigma(d\tilde{s}, d\tilde{z}) \right) \int r P^*(s, dr). \tag{6.16}
\]

Suppose \( \widetilde{\mathcal{H}} \) has the following properties:

(a) If \( \phi_1 \leq \phi_2 \), then \( \widetilde{\mathcal{H}} \phi_1 \leq \widetilde{\mathcal{H}} \phi_2 \).

(b) For any \( \xi \in [0, 1] \) and \( \phi \in \mathcal{M} \), \( \xi \widetilde{\mathcal{H}} \phi \leq \widetilde{\mathcal{H}}(\xi \phi) \).

(c) Suppose \( \widetilde{\mathcal{H}} \) has a non-zero fixed point \( \phi^* \). If \( \int \phi(s, z) \sigma(ds, dz) > 0 \), then there exists a \( \xi \in (0, 1) \) such that \( \xi \phi^* \leq \widetilde{\mathcal{H}} \phi \).

The global stability of the extinction state when \( r(\mathcal{G}) \leq 1 \) follows using the arguments of Busenberg et al. [6, Theorem 5.1]. The stability of the non-zero fixed point when \( r(\mathcal{G}) > 1 \) follows using the arguments of Busenberg et al. [6, Theorem 5.3]. It remains to show that properties (a)-(c) hold for \( \widetilde{\mathcal{H}} \).

To show the monotonicity property (a) holds, note that for any \( \phi \in \mathcal{M} \), \( \int r \phi(r, z) P^*(s, dr) \leq \int r P^*(s, dr) \) for all \((s, z) \in [0, 1] \times \Omega\). Therefore, for any \( \phi_1, \phi_2 \in \mathcal{M} \) such that \( \phi_1 \leq \phi_2 \),

\[
\widetilde{\mathcal{H}} \phi_1(s, z) \leq \left(1 - f \left( \int D(z, \tilde{z}) \phi_2(\tilde{s}, \tilde{z}) \sigma(d\tilde{s}, d\tilde{z}) \right) \right) \int r \phi_1(r, z) P^*(s, dr) \\
+ f \left( \int D(z, \tilde{z}) \phi_2(\tilde{s}, \tilde{z}) \sigma(d\tilde{s}, d\tilde{z}) \right) \int r P^*(s, dr) \\ 
\leq \widetilde{\mathcal{H}} \phi_2(s, z).
\]
For property (b), for any $\xi \in [0, 1]$ and $\phi \in \mathcal{M}$,

$$\tilde{H}(\xi \phi)(s, z) = \left(1 - f \left(\xi \int D(z, \tilde{z})\phi(\tilde{s}, \tilde{z})\sigma(d\tilde{s}, d\tilde{z})\right)\right) \xi \int r\phi(r, z)P^*(s, dr)$$

$$+ f \left(\xi \int D(z, \tilde{z})\phi(\tilde{s}, \tilde{z})\sigma(d\tilde{s}, d\tilde{z})\right) \int rP^*(s, dr),$$

$$\geq \xi \left(1 - f \left(\int D(z, \tilde{z})\phi(\tilde{s}, \tilde{z})\sigma(d\tilde{s}, d\tilde{z})\right)\right) \int r\phi(r, z)P^*(s, dr)$$

$$+ \xi f \left(\int D(z, \tilde{z})\phi(\tilde{s}, \tilde{z})\sigma(d\tilde{s}, d\tilde{z})\right) \int rP^*(s, dr),$$

(6.17)

where inequality (6.17) follows as $f$ is monotone and concave. Therefore, $\xi \tilde{H}\phi \leq \tilde{H}(\xi \phi)$, as required.

To show property (c) holds, note that for any $\phi \in \mathcal{M}$,

$$\tilde{H}\phi(s, z) \geq f \left(\int D(z, \tilde{z})\phi(\tilde{s}, \tilde{z})\sigma(d\tilde{s}, d\tilde{z})\right) \int rP^*(s, dr).$$

By Assumption (C), $\int D(z, \tilde{z})\phi(\tilde{s}, \tilde{z})\sigma(d\tilde{s}, d\tilde{z}) > 0$ for all $z \in \Omega$. By Assumption (J), $\inf_s \int rP^*(s, dr) > 0$. Therefore, $\tilde{H}\phi(s, z) > 0$ for all $(s, z) \in [0, 1] \times \Omega$. As $[0, 1] \times \Omega$ is closed, and $\phi^*$ is bounded, there exists a $\xi \in (0, 1)$ such that $\xi \phi^* \leq \tilde{H}\phi$.

**REFERENCES**

[1] Akçakaya HR, and Ginzburg LR (1991) Ecological risk analysis for single and multiple populations, pages 78-87 in Species Conservation: A Population Biological Approach (Seitz A and Loeschcke V, eds.), Birkhauser, Basel

[2] Akçakaya HR, Radeloff VC, Mladenoff DJ, and He HS (2004) Integrating landscape and metapopulation modeling approaches: Viability of the sharp-tailed grouse in a dynamic landscape, Conservation Biology, 18, 526-537

[3] Arnold L (1998) Random Dynamical Systems, Springer, New York

[4] Bebbington M, Pollett PK and Zheng X (1995) Dual constructions for pure-jump Markov processes, Markov Processes and Related Fields, 1, 513-558

[5] Boyle OD, Menges ES and Waller DM (2003) Dances with fire: Tracking metapopulation dynamics of *Polygonella Basiramia* in Florida scrub (USA), Folia Geobotanica, 38, 255-262

[6] Busenberg SN, Iannelli M and Thieme HR (1991) Global behavior of an age-structured epidemic model, SIAM Journal on Mathematical Analysis, 22, 1065-1080
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[7] Cornell SJ and Ovaskainen O (2008) Exact asymptotic analysis for metapopulation dynamics on correlated dynamic landscapes, Theoretical Population Biology, 74, 209-225

[8] Day JR and Possingham HP (1995) A stochastic metapopulation model with variability in patch size and position, Theoretical Population Biology, 48, 333-360

[9] Durrett R (2010) Random Graph Dynamics, Cambridge University Press, New York

[10] Gregg L, and Niemuth ND (2000) The history, status, and future of the sharp-tailed grouse in Wisconsin, The Passenger Pigeon 62:159-174

[11] Hanski I (1994) A practical model of metapopulation dynamics, Journal of Animal Ecology, 63, 151-162

[12] Hanski I (1999) Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes, Oikos, 87, 209-219

[13] Hansi I and Ovaskasinen O (2003) Metapopulation theory for fragmented landscapes, Theoretical Population Biology, 64, 119-127

[14] Hill MF and Caswell H (2001) The effects of habitat destruction in finite landscapes: A chain-binomial metapopulation model, Oikos, 93, 321-331

[15] Hirsch MW and Smith H (2005) Monotone maps: A review, Journal of Difference Equations and Applications, 11, 379-398

[16] Johansson V, Ranius T and Snäll T (2012) Epiphyte metapopulation dynamics are explained by species traits, connectivity, and patch dynamics, Ecology, 93, 235-241

[17] Kallenberg O (2002) Foundations of modern probability, 2nd edn. Springer, New York

[18] Keymer JE, Marquet PA, Velasco-Hernández JX and Levin SA (2000) Extinction thresholds and metapopulation persistence in dynamic landscapes, The American Naturalist, 156, 478-494

[19] Krein MG and Rutman MA (1950) Linear operators leaving invariant a cone in a Banach space, American Mathematical Society Translation, number 26, 128 pp.

[20] Kress R (1989) Linear Integral Equations, Springer-Verlag, New York

[21] McVinish R and Pollett PK (2010) Limits of large metapopulations with patch-dependent extinction probabilities, Advances in Applied Probability, 42, 1172-1186

[22] McVinish R and Pollett PK (2012) The limiting behaviour of a mainland-island metapopulation, Journal of Mathematical Biology, 64, 775-801
[23] McVinish R and Pollett PK (2013) The limiting behaviour of a stochastic patch occupancy model, Journal of Mathematical Biology, 67, 693-716
[24] McVinish R and Pollett PK (2013) The deterministic limit of a stochastic logistic model with individual variation, Mathematical Biosciences, 241, 109-114
[25] McVinish R and Pollett PK (2013) Interaction between habitat quality and an Allee-like effect in metapopulations, Ecological Modelling, 249, 84-89
[26] McVinish R and Pollett PK (2014) The limiting behaviour of Hanks’s incidence function metapopulation model, Journal of Applied Probability, 51, 297-316
[27] Meyn SP and Tweedie RL (1996) Markov Chains and Stochastic Stability, Springer-Verlag, London.
[28] Ovaskainen, O (2001) The quasistationary distribution of the stochastic logistic model, Journal of Applied Probability, 38, 898-907
[29] Ovaskainen O and Hanski I (2001) Spatially structured metapopulation models: Global and local assessment of metapopulation capacity, Theoretical Population Biology, 60, 281-302
[30] Ovaskainen O and Hanski I (2004) Metapopulation dynamics in highly fragmented landscapes, pages 73-103 in Biology, Genetics, and Evolution of Metapopulations. (Hanski I and Gaggiotti OE, eds.), Elsevier, Burlington
[31] Ranga Rao, R (1962) Relations between weak and uniform convergence of measures with applications, Annals of Mathematical Statistics, 33, 659-680
[32] Ranius T, Bohman P, Hedgren O, Wikars L-O and Caruso A (2014) Metapopulation dynamics of a beetle species confined to burned forest sites in a managed forest region, Ecography 37, 797-804
[33] Ross JV (2006) A stochastic metapopulation model accounting for habitat dynamics, Journal of Mathematical Biology, 52, 788-806
[34] van Teeffelen AJA, Vos CC and Opdam P (2012) Species in a dynamic world: Consequences of habitat dynamics on conservation planning, Biological Conservation, 153, 239-253
[35] Verheyen K, Vellend M, Van Calster H, Peterken G and Hermy M (2004) Metapopulation dynamics in changing landscapes: A new spatially realistic model for forest plants, Ecology, 85, 3302-3312
[36] Watson JR, Kendall BE, Siegel DA and Mitarai S (2012) Changing seascapes, stochastic connectivity, and marine metapopulation dynamics, The American Naturalist, 180, 99-112

[37] Weiss GH and Dishon M (1971) On the asymptotic behaviour of the stochastic and deterministic models of an epidemic, Mathematical Biosciences, 11, 261-265

[38] Wilcox C, Cairns BJ and Possingham HP (2006) The role of habitat disturbance and recovery in metapopulation persistence, Ecology, 87, 855-863

[39] Xu D, Feng Z, Allen LJS, Shiwart RK (2006) A spatially structured metapopulation model with patch dynamics, Journal of Theoretical Biology, 239, 469-481