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

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

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

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ABSTRACT

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

1. Introduction

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

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

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

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

Using the differential equation, we are able to determine conditions under which the metapopulation will go extinct quickly or persist for an extended period of time. We are also able to identify more complex dynamics such as the presence of an Allee effect for some range of parameters. An Allee effect refers to populations exhibiting an increasing per capita growth rate at low population density levels. When the per-capita growth rate is initially

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* Corresponding author. Tel.: +61 413491147.
E-mail addresses: a.smith23@uq.edu.au, agsmith87@live.com (A.G. Smith).

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negative, a critical threshold emerges below which the population goes extinct. In populations displaying an Allee effect, conservation strategies need to be adapted to account for this, particularly if a critical threshold is present [25, Section 5.1.4].

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

2. The model

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

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

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

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

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

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

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

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

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

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

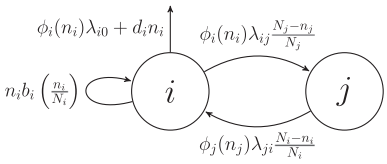

Fig. 1. Illustration of the dynamics for patch i and migration to and from patch j.

3. Differential equation approximation

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

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

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

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

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

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

where

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

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

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

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

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

and also

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

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

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

for $i = 1, \ldots, J$. Therefore, the family of processes indexed by the population ceiling N is asymptotically density dependent according to Definition 3.1 of [24]. Next we apply Theorem 3.1 of [24], the analogue of Theorem 3.1 of Kurtz [23] for asymptotically density dependent families of processes. The conditions of this theorem are fulfilled as $f_N(x, l)$ is bounded on E for all N and l and is nonzero