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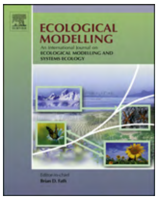

Analytical methods for a stochastic mainland–island metapopulation model

F.M. Buckley*, P.K. Pollett

Department of Mathematics, University of Queensland, St Lucia, Qld 4072, Australia

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ABSTRACT

We study a class of chain-binomial metapopulation models, giving special attention to the 'mainland–island' configuration, where patches receive immigrants from an external source. We evaluate the distribution of the number n_t of occupied patches at any census time t and establish a law of large numbers that identifies a deterministic trajectory which can be used to approximate the process when the number of patches is large. We also establish a central limit law, which shows that the fluctuations about this trajectory are approximately normally distributed. We describe briefly much finer results that can be used for model calibration.

1. Introduction

The term 'metapopulation' is used to describe individuals of a species living as a group of local populations in geographically separate, but connected, habitat patches (Levins, 1970; Hanski, 1999). Patches may become empty through local extinction and empty patches may be recolonised by immigrants from other local populations. A balance between local extinction and colonisation may be reached which allows the metapopulation to persist (Hanski, 1999). The relationship between these two processes is therefore an important consideration when formulating mathematical metapopulation models. We suppose that events of the same type occur in seasonal *phases*, so that extinction events only occur during the *extinction phase* and colonisation events only occur during the *colonisation phase*, and that these phases alternate over time. They may correspond to two parts of an annual cycle, for example, where local populations are prone to extinction during winter whilst new populations establish during spring.

We assume that a census takes place either at the end of the colonisation phase (...–extinction–colonisation–census–...) or at the end of the extinction phase (...–colonisation–extinction–census–...), and thus fits naturally within a discrete-time modelling framework. If extinction and colonisation events were to occur in random order, then a continuous-time model would of course be preferred. Here we use a discrete-time Markov chain whose state n_t is the observed number of occupied patches at the t-th census. Its transition matrix is the product of two transition matrices that govern the individual extinction and colonisation processes. This approach has been used previously and several models have been proposed (Akçakaya and Ginzburg, 1991; Day and Possingham, 1995; Hill and Caswell, 2001; Klok and De Roos, 1998; Tenhumberg et al., 2004; Rout et al., 2007). Each model accounts for local extinction in the same way, but different methods are used to model the colonisation process, reflecting the differing breeding habits and means of propagation of the particular species under investigation. Whilst they account for a range of colonisation behaviour, the models were examined using numerical methods and simulation, and few explicit analytical results were obtained. Furthermore, only the extinction–colonisation–census scenario was considered. Whilst it is certainly true that timing of the census is arbitrary in that it does not affect the dynamics of the metapopulation (Day and Possingham, 1995), its timing may affect the efficiency of any statistical procedures used to calibrate the models and successful implementation of management actions.

We present a new and quite general approach to modelling the colonisation process, one that permits explicit expressions for a variety of quantities of interest. We concentrate here on a *mainland–island* configuration: the patches (*islands*) receive immigrants from an external source (the *mainland*), assumed to be immune from extinction. We evaluate the distribution of n_t at any census time t. We then establish a *law of large numbers* that identifies a deterministic trajectory which can be used to approximate $(n_t, t \geq 0)$ at any time t when the number of patches is large. We also establish a *central limit law*, which shows that the fluctuations about this trajectory are approximately normally distributed. These results are useful in understanding the patch-occupancy process when the parameters of the model are known. For example, the mean and variance of n_t, and the expected time to first total extinction, can be exhibited explicitly. We describe briefly much finer results that can be used for model calibration.

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* Corresponding author. Tel.: +61 7 3346 1427; fax: +61 7 3365 1477.
E-mail addresses: fbuckley@maths.uq.edu.au (F.M. Buckley), pkp@maths.uq.edu.au (P.K. Pollett).

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2. Patch-occupancy models

Stochastic patch-occupancy models (SPOMs) which assume that extinction and colonisation occur in distinct phases in discrete-time can be categorised as (i) heterogeneous SPOMs (Akçakaya and Ginzburg, 1991; Day and Possingham, 1995) or (ii) homogeneous SPOMs (Daley and Gani, 1999; Hill and Caswell, 2001; Klok and De Roos, 1998; Rout et al., 2007; Tenhumberg et al., 2004). Heterogeneous SPOMs use a vector of size N to describe the presence/absence of occupants in an N-patch metapopulation, the k-th component being 1 or 0 according to whether the k-th patch is occupied or empty. Local extinction and colonisation event probabilities can be patch-specific, such as in Akçakaya and Ginzburg's (1991) 3-patch model for the endangered Mountain Gorilla (*Gorilla gorilla beringei*) metapopulation in Uganda, or vary according to patch size and position as demonstrated in Day and Possingham's (1995) 8-patch model for the malleefowl (*Leipoa ocellata*) metapopulation in South Australia. Since there are 2^N possible states, the analysis of these models quickly becomes computationally expensive as N increases. Homogeneous SPOMs on the other hand simply record the number of occupied patches and therefore have only $N+1$ states for an N-patch metapopulation, entailing computationally inexpensive analysis even for large ($N = 50$) networks. Whilst patches are assumed to behave in the same way, these models can account implicitly for spatial arrangement by allowing the colonisation probabilities to depend on the number of occupied patches. They have additional appeal because, as we shall see, they can be analytically tractable. Two-phase homogeneous SPOMs are usually based on the following approach to modelling the extinction and colonisation processes.

2.1. Extinction and colonisation

Occupied patches are assumed to go extinct independently, each with the same probability e. Hence, given i patches initially occupied, the number that survive the extinction process follows a binomial $\mathrm{Bin}(i, 1-e)$ law. With j patches remaining after the extinction phase, the $N-j$ empty patches either remain empty or are colonised during the subsequent colonisation phase. In modelling the colonisation process one must consider how individuals disperse through the metapopulation network. Hill and Caswell (2001) assume implicitly that propagules arrive at each patch according to a homogeneous Poisson process with rate $\beta i/N$, where i is the number of patches currently occupied and β is the expected number of propagules produced by each occupied patch. Thus, the probability that one or more propagules arrive at any given patch is $c_i = 1 - \exp(-\beta i/N)$, and so the number of colonisation events follows a binomial $\mathrm{Bin}(N-i, c_i)$ law. Their model goes one step further in allowing only a fixed subset of the N patches to be suitable for habitation.

Klok and De Roos (1998) suppose that colonisation comprises two separate processes: (i) reproduction, which determines the number of juveniles born to adults that survive the preceding extinction phase (each adult occupying one patch or 'territory'), and (ii) settlement, which determines how many patches are colonised by juveniles. Each process is governed by its own transition matrix and these are multiplied to produce the overall transition matrix for the colonisation phase. Their model was designed to study the common shrew (*Sorex araneus* L.), which exhibits the three-phase (extinction–reproduction–settlement) behaviour described.

Tenhumberg et al. (2004) and Rout et al. (2007) model a single population of individuals with an assumed fixed population ceiling. Their models track the number of female individuals, each producing either a maximum of one offspring (Tenhumberg et al., 2004), or a binomially distributed number of offspring (Rout et al., 2007). The total number of females resulting from the colonisation process is then determined by a recursive formula.

These Markov chain models are often referred to as *chain-binomial models* (Daley and Gani, 1999; Hill and Caswell, 2001), because the numbers of patches/individuals remaining after each phase is determined by a binomial distribution whose parameters are determined by the result of the previous phase.

2.2. Timing of the census

Whilst the choice between taking the census after colonisation or after extinction does not affect the dynamics of the metapopulation, it is certainly important from an empirical perspective. For example, Klok and De Roos (1998) chose to census after the colonisation phase because the real shrew population was known to be more stable at this time.

Our approach is similar. We introduce a homogeneous stochastic patch-occupancy model of a similar design to those described, but with a quite general approach to modelling colonisation. We study both census scenarios and present analytical results for both, concentrating here on the mainland–island configuration.

3. A chain-binomial model with state dependent colonisation probabilities

Suppose there are N patches. Let n_t be the observed number occupied at census time $t \in \{0, 1, \ldots\}$ and suppose that $(n_t, t \geq 0)$ is a discrete-time Markov chain that takes values in $S = \{0, 1, \ldots, N\}$ with transition probabilities $P = (p_{ij})$. The colonisation and extinction processes are governed by their own transition matrices, $E = (e_{ij})$ and $C = (c_{ij})$, respectively, so that $P = EC$ (the EC model) if the census is taken just after the colonisation phase or $P = CE$ (the CE model) if the census is taken just after the extinction phase.

3.1. Extinction phase

Occupied patches are assumed to go extinct independently, each with the same probability e $(0 < e < 1)$. Thus, given i occupied at the start of the extinction phase, the number that survive extinction follows a $\mathrm{Bin}(i, 1-e)$ law. Therefore

$$e_{ij} = \binom{i}{j}(1-e)^j e^{i-j}, \qquad \text{for} j = 0, \ldots, i,$$

and $e_{ij} = 0$ for $j > i$.

3.2. Colonisation phase

Suppose that, given i occupied patches at the start of the colonisation phase, the empty patches are colonised independently, each with probability c_i $(0 < c_i < 1)$. We call c_i the colonisation potential (of i occupied patches). Thus, given i occupied (and hence $N-i$ unoccupied), the number of empty patches colonised during this phase follows a $\mathrm{Bin}(N-i, c_i)$ law. Therefore,

$$c_{ij} = \binom{N-i}{j-i}(1-c_i)^{N-j} c_i^{j-i}, \qquad \text{for} \quad j = i, i+1, \ldots, N,$$

and $c_{ij} = 0$ for $j < i$. This general setup accommodates (among other choices):

(i) $c_i = 1 - \exp(-\beta i/N)$, which is Hill and Caswell's (2001) specification with β being the propagation rate;
(ii) $c_i = (i/N)c$, where the colonisation potential is *proportional to* the number of occupied patches up to a fixed maximum colonisation potential $c \in (0, 1]$, the (hypothetical) probability that a