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Limits for density dependent time inhomogeneous Markov processes

Andrew G. Smith*

School of Mathematical Sciences, University of Adelaide, SA 5005, Australia

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ABSTRACT

A new functional law of large numbers to approximate a time inhomogeneous Markov process that is only density dependent in the limit as an index parameter goes to infinity is developed. This extends previous results by other authors to a broader class of Markov processes while relaxing some of the conditions required for those results to hold. This result is applied to a stochastic metapopulation model that accounts for spatial structure as well as within patch dynamics with the novel addition of time dependent dynamics. The resulting nonautonomous differential equation is analysed to provide conditions for extinction and persistence for a number of examples. This condition shows that the migration of a species will positively impact the reproduction in less populated areas while negatively impacting densely populated areas.

1. Introduction

A metapopulation is a population that is separated into geographically distinct patches which allow migration between patches. Many metapopulation models assume that the underlying environment the population inhabits is static [5,10,19,22]. Such an assumption is often made for one or both of the following reasons: firstly, the variation of the environment is often sufficiently small that it can be neglected; and, secondly, models with static environments are significantly more tractable. However, if the variation of the environment is not sufficiently small, any predictions based on a model that fails to account for this variation could be highly inaccurate. In this situation, tractability needs to be improved.

To accomplish this, deterministic approximations are often used [6,11,18,25]. Besides simplifying the analysis, deterministic models are a useful way to approximate the mean of quasi-stationary distributions; the stationary distribution of the stochastic process conditioned on not being absorbed [4]. One of the models that uses a deterministic approximation is given by Smith et al. [25], where a spatially structured metapopulation model that accounts for within patch dynamics via a birth–death–migration process is introduced. The results of Pollett [23] for asymptotically density dependent Markov processes were then applied, which resulted in a limiting system of differential equations that approximated the mean trajectory of the stochastic process.

While Smith et al. allowed the dynamics on each patch to be heterogenous, dynamics such as births and migrations can often not only vary spatially but temporally also, in the form of breeding and migration seasons, for example. Furthermore, this variation is not limited to merely the births and migrations, but nearly all dynamics included in the model can often varying temporally also. To account for such behaviour, a time inhomogeneous Markov process will be used to model the number of individuals on each patch. However, the results of Pollett [23] do not hold for such models, and even the more recent work of Pagendam and Pollett [20] fails to account for inhomogeneous models of the form given in [25].

To begin, an extension to the model by Smith et al. [25] is introduced, which accounts for temporally varying parameters. In Section 3, a new functional law of large numbers is proposed, one that can be applied to inhomogeneous asymptotically density dependent Markov chains (Theorem 3.2), a class which includes the model presented in Section 2. The approximating differential equation resulting from the functional law of large numbers is examined in Section 4 and conditions for extinction and persistence are presented.

2. Model

Let J be the number of patches that can be occupied in the metapopulation, and $n_i^{(N)}(t)$ be the number of individuals occu-

* Tel.: +61883133245.
E-mail address: andrew.smith01@adelaide.edu.au

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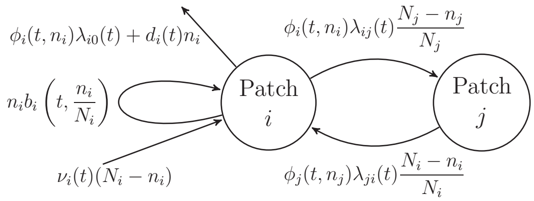

Fig. 1. Illustration of the dynamics for patch i and migration to and from patch j, where the edges of the graph illustrate possible individual movements.

pying patch i at time t, and define $n^{(N)}(t) := \{n_1^{(N)}(t), \dots, n_J^{(N)}(t)\}$, indexed by N which is the total population ceiling. The birth–death–migration process $(n^{(N)}(t), t \ge 0)$ takes values in the state space $S_N := \{0, \dots, N_1\} \times \cdots \times \{0, \dots, N_J\}$, where N_i is the population ceiling for patch i, noting the relation $N = \sum_i N_i$. Furthermore, the environment which the metapopulation inhabits is allowed to vary by adopting transition rates that have explicit time dependence. Then the process $(n^{(N)}(t), t \ge 0)$ has nonzero transition rates

$$q(n, n+e_i; t) = \nu_i(t)(N_i - n_i) + n_i b_i\left(t, \frac{n_i}{N_i}\right), \tag{1a}$$

$$q(n, n-e_i; t) = \phi_i(t, n_i)\lambda_{i0}(t) + d_i(t)n_i, \tag{1b}$$

$$q(n, n-e_i+e_j; t) = \phi_i(t, n_i)\lambda_{ij}(t)\frac{N_j - n_j}{N_j} \quad \text{for all } j \ne i, \tag{1c}$$

where e_i is the unit vector with a 1 in the ith position. These rates correspond to: an increase on patch i due to a birth or external immigration (1a), a decrease on patch i due to a death or removal from the system (1b) and a migration from patch i to patch j (1c), all at time t. The birth rate function $b_i(t, \cdot)$ determines the per-capita birth rate at time t given how densely populated patch i is. The functions $\nu_i(t)$, $d_i(t)$ and $\lambda_{ij}(t)$ are the external immigration rate, per-capita death rate function and proportion of individuals migrating from patch i to patch j (or out of the system if $j = 0$) at time t for patch i, respectively. The migration function $\phi_i(t, \cdot)$ represents the rate at which individuals leave patch i at time t. Fig. 1 illustrates the transitions (1).

3. Functional limit law

First, it is to be noted that the transition rates (1) can be written in the form

$$q(n, n+l; t) = Nf^{(N)}\left(t, \frac{n}{N}, l\right),$$

where $l \in \mathbb{Z}^J$ represents possible jumps and

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

$M_i^{(N)} := N_i/N$, and the functions $\hat{\phi}_i^{(N)} : [0, \infty) \times [0, M_i^{(N)}] \to \mathbb{R}_+$ satisfy

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

In the definition of density dependence by Kurtz [16], there is an equivalent function, $f(x, l)$, to the function $f^{(N)}(t, x, l)$ given above. However, one will note that f does not have any dependence on t or N and, as such, the process $n^{(N)}(t)$ is not density dependent. Furthermore, $f^{(N)}(x, l)$ (which is equivalent to $f^{(N)}(t, x, l)$) in Definition 3.1 of [23] has no dependence on t, while $f(t, x, l)$ in Definition 1 of [20] has no dependence on N. So again, the process $n^{(N)}(t)$ is not density dependent according to either of these definitions. Therefore, it is necessary to extend these definitions to include a new type of process: an *asymptotically* density dependent process *in time*.

Definition 3.1. A family of Markov processes $\{n^{(N)}(t)\}$ indexed by $N > 0$ (with a state space $S_N \subset \mathbb{Z}^J$) is said to be "*asymptotically* density dependent in time" if there exists a continuous function, $f^{(N)} : [0, \infty) \times E \times \mathbb{Z}^J \mapsto \mathbb{R}$, where $E \subseteq \mathbb{R}^J$, such that the transition rates of $n^{(N)}(t)$ are given by

$$q\left(n^{(N)}, n^{(N)} + l; t\right) = Nf^{(N)}\left(t, \frac{n^{(N)}}{N}, l\right), \quad l \ne 0,$$

and $F^{(N)}(t, x) := \Sigma_l l f^{(N)}(t, x, l)$ converges uniformly over $[0, \infty) \times E$ to $F(t, x)$ as $N \to \infty$.

The process with rates (1) satisfies Definition 3.1 under some additional mild assumptions. Assume that $M_i^{(N)} \to M_i$ and there exists functions $\hat{\phi}_i : S_i \mapsto \mathbb{R}_+$, where $S_i := [0, \infty) \times [0, M_i]$, satisfying

$$\lim_{N\to\infty} \sup_{(t,x)\in S_i} \left|\hat{\phi}_i^{(N)}(t, x) - \hat{\phi}_i(t, x)\right| = 0, \quad \text{for all } i, \tag{2}$$

and also functions $b_i : [0, \infty) \times [0, 1] \mapsto \mathbb{R}_+$ satisfying

$$\lim_{N\to\infty} \sup_{(t,x)\in S_i} \left|b_i\left(t, \frac{x_i}{M_i^{(N)}}\right) - b_i\left(t, \frac{x_i}{M_i}\right)\right| = 0, \quad \text{for all } i. \tag{3}$$

Then, if the total population ceiling, N, is taken as the index parameter and $E = [0, M_1] \times \cdots \times [0, M_J]$, the process with rates (1) is asymptotically density dependent in time according to Definition 3.1. Just as the definition of density dependence was extended to include asymptotic density dependence in time, Theorem 1 of [20] needs to be extended to also include asymptotically density dependent processes. This extension, presented in Theorem 3.2 below, relaxes the condition of E being an open set which is imposed in all previous results. While conditions (B) and (C) below are also different conditions than required previously, the difference is not significant. Informally, as N gets large, the density process, $n^{(N)}(t)/N$, converges to the solution of a differential equation.

Theorem 3.2. *Let $(n^{(N)}(t), t \ge 0)$, indexed by N, be asymptotically density dependent in time. Furthermore, assume that*

(A) *F is Lipschitz,*
(B) $\sup_{x\in E} \sum_l f^{(N)}(t, x, l) < \infty$, *for all $t > 0$, $N \ge 1$ and*
(C) $\sup_{x\in E} \sum_l |l|^2 f^{(N)}(t, x, l) < \infty$ *for all $t > 0$, $N \ge 1$,*

where the product $|\cdot|^2$ is the Euclidean norm of the element-wise product. Then if $n^{(N)}(0)/N \to x_0$ in probability as $N \to \infty$ then, for any $\varepsilon > 0$ and for all fixed $t > 0$,

$$\lim_{N\to\infty} \mathbb{P}\left(\sup_{s\le t} \left|\frac{n^{(N)}(s)}{N} - x(s, x_0)\right| > \varepsilon\right) = 0, \tag{4}$$

where $x(t, x_0)$ is the solution to

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

Proof. Define $X^{(N)}(t) := n^{(N)}(t)/N$. Under the conditions of Theorem 7.3 of [9], $X^{(N)}(t)$ may be expressed as

$$X^{(N)}(t) = X^{(N)}(0) + M^{(N)}(t) + \int_0^t F^{(N)}(s, X^{(N)}(s))ds, \tag{5}$$

where $M^{(N)}(t)$ is a martingale with respect to the filtration $\mathcal{F}_t^{(N)} = \sigma\{X^{(N)}(s), 0 \le s \le t\}$. To verify the conditions of Theorem 7.3 of [9], set

$$\mu(t, x, y) = \frac{Nf^{(N)}(t, x, y - x)}{\lambda(t, x)} \quad \text{and} \quad \lambda(t, x) = N\sum_l f^{(N)}(t, x, l)$$