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PARALLEL MUTATION-REPRODUCTION PROCESSES IN RANDOM ENVIRONMENTS

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ABSTRACT. We introduce parallel mutation-reproduction processes in random environments to model the evolution of structured populations in uncertain environments. The existence of such processes is shown in a general framework. We show that populations in an important class of such models may undergo global expansion or tend to extinction.

1. Introduction

To study the evolution of populations in a random environment, there are two basic types of models. One is where the underlying dynamics is deterministic; see [6] for the case of structured populations in discrete time. For the other, the underlying dynamics is given by a branching process. The importance of a random environment on the growth of a single type population has been known for some time for both models, see for example [13].

There is a rich literature on branching processes both in theory and in application, such as [11, 4, 14, 10]. These include results about branching processes in a random environment. For multitype branching processes in a random environment, the literature has been mainly restricted to the discrete time case, i.e. to the Galton-Watson processes [1, 2, 3]. Our model will be a special *continuous* time multitype Markov branching process in a random environment.

Parallel mutation-reproduction processes were introduced by Baake and Georgii in [5] as a simple model of the evolution of structured populations. Here we wish to consider the effect of random environments on the developments of such structured populations.

First, we construct a general d-type Markov branching process in a random environment, denoted by $\{\mathbf{Z}(t) = (Z^1(t), \cdots, Z^d(t))^\top\}_{t\geq 0}$, by employing the technique used in ([9], Chap. 6.4 and Chap. 9.3). The process $\{\mathbf{Z}(t)\}_{t\geq 0}$ takes values in $\mathbb{Z}_+^d = \{\mathbf{n} = (n_1, \cdots, n_d)^\top \mid n_i \text{ nonnegative integer}\}$. It is constructed as the solution of

$$\mathbf{Z}(t) = \mathbf{Z}(0) + \sum_{\alpha\in\tilde{\mathbb{Z}}_+^d} \alpha Y_\alpha \left(\int_0^t \Lambda_\alpha(s)\cdot \mathbf{Z}(s)\mathrm{d}s \right), \tag{1.1}$$

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where $\tilde{\mathbb{Z}}_+^d = \bigcup_{i=1}^d \{\mathbf{n} - e_i \mid \mathbf{n} \in \mathbb{Z}_+^d\}$ with e_i denoting a column vector with ith component equal to 1 and others 0, $\{\Lambda_\alpha = (\Lambda_{\alpha+e_1}^{(1)}, \cdots, \Lambda_{\alpha+e_d}^{(d)})^\top,\ \alpha \in \tilde{\mathbb{Z}}_+^d\}$ are splitting intensities of the multitype Markov branching process in a random environment, and $\{Y_\alpha,\ \alpha \in \tilde{\mathbb{Z}}_+^d\}$ are independent standard Poisson processes, independent of the $\mathbb{R}_+^d$-valued processes $\{\Lambda_\alpha,\ \alpha \in \tilde{\mathbb{Z}}_+^d\}$. An explanation of these concepts and (1.1) are given in section 2. We assume that $\sum_{\alpha \in \tilde{\mathbb{Z}}_+^d} \alpha_j \int_0^t \Lambda_{\alpha+e_i}^{(i)}(s)\mathrm{d}s < \infty$ a.s. for all $t \geq 0$ and each $i, j = 1, \cdots, d$. The assumption ensures that the solution of (1.1) exists for all the time and is unique a.s.

In order to explore the long time behaviour of such models, we consider a two-type parallel mutation-reproduction Markov branching process in a random environment, still denoted by $\{\mathbf{Z}(t)\}_{t\geq 0}$. Assume that the splitting intensities $\{\Lambda_\alpha,\ \alpha \in \tilde{\mathbb{Z}}_+^2\}$ are all controlled by the same environmental process $\{\eta(t)\}_{t\geq 0}$, which is an irreducible, recurrent Markov chain in continuous time on a countable state space $\mathcal{Y}$. Extending results of Cogburn and Torrez [8], we show the instability property of $\{\mathbf{Z}(t)\}_{t\geq 0}$, i.e., $\mathrm{P}_{(y,\mathbf{z})}\{\lim_{t\to\infty} \|\mathbf{Z}(t)\|_1 = 0 \text{ or } \infty\} = 1$, for every $(y, \mathbf{z}) \in \mathcal{Y} \times \mathbb{Z}_+^2$, given some additional technical conditions.

The paper is organised as follows. In section 2, we give a rigorous construction of multitype Markov branching processes in random environments. In section 3, we analyse the instability property of a parallel mutation-reproduction Markov branching process in a random environment. In the results of section 2 the randomness of the environment plays essentially no role, and the environment could be treated as fixed. However, in section 3 the behaviour of the environment is crucial.

In a sequel, we will prove a weak convergence result for a sequence of parallel Markov branching processes in random environments [18]. This makes use of the approach to the construction of such processes described here as well as their asymptotic behaviour.

2. Construction

A continuous-time one-type Markov branching process in a random environment is defined as a solution of a stochastic equation involving Poisson processes by Ethier and Kurtz ([9], Chap.9.3). We will generalize the construction above to a continuous-time multitype Markov branching process in a random environment, denoted by $\{\mathbf{Z}(t)\}_{t\geq 0}$. We postulate that when conditioned on the random environment, $\{\mathbf{Z}(t)\}_{t\geq 0}$ behaves as a continuous-time non-homogeneous vector-valued Markov branching process. Processes of this type are briefly discussed in Chap.5 of [11] and the references therein. Here we give full proofs, for the sake of completeness, and put them in the random environment context.

Recall that a continuous-time non-homogeneous d-type Markov branching process is mainly determined by the *splitting rate* $\lambda^{(i)}(t)$ and *offspring distribution* $\{p_\gamma^{(i)}(t)\}_{\gamma \in \mathbb{Z}_+^d}$ of an individual of type i at time t. Here i belongs to the type space $S = \{1, \cdots, d\}$. The splitting rate $\lambda^{(i)}(t)$ means that an individual of type i has a probability $\lambda^{(i)}(t)\Delta t + o(\Delta t)$ of dying in the interval $(t, t + \Delta t)$. Also $p_\gamma^{(i)}(t)$ (for

$\gamma = (\gamma_1, \cdots, \gamma_d)^\top$) is the probability that an individual of type i has γ_j offspring of type j (for $j = 1, \cdots, d$) at time t.

In random environment, both the splitting rates and offspring distributions become random processes. The environment is modelled by a process $\{\eta(t)\}_{t\geq 0}$, the *environmental process*, which we can take to be vector-valued and defined on a probability space $(\Omega_R, \mathcal{F}_R, \mathrm{P}_R)$. The splitting rate $\lambda^{(i)}$ and offspring distribution $\{p_\gamma^{(i)}\}_{\gamma\in\mathbb{Z}_+^d}$ are taken to be stochastic processes on $(\Omega_R, \mathcal{F}_R, \mathrm{P}_R)$ which are adapted to $\mathcal{F}_t^\eta := \sigma\{\eta(s) : 0 \leq s \leq t\}$. We write $\lambda^{(i)}(t,\omega)$ and $\{p_\gamma^{(i)}(t,\omega)\}_{\gamma\in\mathbb{Z}_+^d}$ for the splitting rate and offspring distribution in the realisation $\omega \in \Omega_R$.

Define the *splitting intensities* of the Markov branching process in a random environment as $\Lambda_\gamma^{(i)}(t,\omega) = \lambda^{(i)}(t,\omega)p_\gamma^{(i)}(t,\omega)$, for $i \in S$ and $\gamma \in \mathbb{Z}_+^d$. Note that $\Lambda_\gamma^{(i)}$, for $i \in S$ and $\gamma \in \mathbb{Z}_+^d$, are themselves nonnegative stochastic processes defined on $(\Omega_R, \mathcal{F}_R, \mathrm{P}_R)$. Let e_i denote a column vector with ith component equal to 1 and others 0. It is customary to only consider splitting intensities with $\Lambda_{e_i}^{(i)} = 0$ for each $i \in S$, i.e., we omit the possibility of a death of an individual followed by replacement by itself since this represents no change in the situation because of the lack of dependence on age.

Before stating the construction of a d-type Markov branching process in a random environment, we first give some notation. Recall $\tilde{\mathbb{Z}}_+^d = \bigcup_{i\in S}\{\mathbf{n} - e_i \mid \mathbf{n} \in \mathbb{Z}_+^d\}$. For each $\alpha \in \tilde{\mathbb{Z}}_+^d$, write $\Lambda_\alpha = (\Lambda_{\alpha+e_1}^{(1)}, \cdots, \Lambda_{\alpha+e_d}^{(d)})^\top$. It is conventional to consider $\Lambda_{\alpha+e_i}^{(i)} = 0$, for $\alpha + e_i \notin \mathbb{Z}_+^d$. Write $\Lambda = \{\Lambda_\alpha,\ \alpha \in \tilde{\mathbb{Z}}_+^d\}$. Write $\mathbf{Z}(t) = (Z^1(t), \cdots, Z^d(t))^\top$, where $Z^i(t)$ stands for the number of individuals of type i at time t. Write $\Lambda_\alpha \cdot \mathbf{Z} = \sum_{j\in S} \Lambda_{\alpha+e_j}^{(j)} Z^j$.

Let $\{Y_\alpha,\ \alpha \in \tilde{\mathbb{Z}}_+^d\}$ be independent standard Poisson processes defined on a probability space $(\Omega_B, \mathcal{F}_B, \mathrm{P}_B)$. In particular, for each $\alpha \in \tilde{\mathbb{Z}}_+^d$, the process $\{Y_\alpha(t)\}_{t\geq 0}$ is integer-valued with starting point $Y_\alpha(0) = 0$, cadlag, non-decreasing, with unit jumps, and stationary and independent increments such that $\mathrm{E}\big[|Y_\alpha(t) - Y_\alpha(s)|\big] = |t-s|$. Note that such a Poisson process can be time changed by a non-decreasing process ρ to give a process $\{Y_\alpha(\rho(t))\}_{t\geq 0}$ whose jumps are still of unit magnitude but which occur more or less frequently as dictated by ρ.

Let $(\Omega, \mathcal{F}, \mathrm{P}) = (\Omega_R \times \Omega_B, \mathcal{F}_R \times \mathcal{F}_B, \mathrm{P}_R \times \mathrm{P}_B)$ be the product probability space. Note that $\{Y_\alpha,\ \alpha \in \tilde{\mathbb{Z}}_+^d\}$ are independent of Λ on $(\Omega, \mathcal{F}, \mathrm{P})$. By employing the technique used in ([9], Chap.6.4 and Chap.9.3), we define a d-type Markov branching process $\{\mathbf{Z}(t)\}_{t\geq 0}$ in a random environment $\{\eta(t)\}_{t\geq 0}$ on $(\Omega, \mathcal{F}, \mathrm{P})$ as the solution of

$$\mathbf{Z}(t) = \mathbf{Z}(0) + \sum_{\alpha\in\tilde{\mathbb{Z}}_+^d} \alpha Y_\alpha \left(\int_0^t \Lambda_\alpha(s) \cdot \mathbf{Z}(s)\mathrm{d}s \right). \tag{2.1}$$

This equation is designed to model the fact that the changes in the population are given by jumps of different sizes whose frequency is determined by the existing population of all types and their splitting intensities moderated by the environment. We will impose a condition to ensure the sums converge. Of course in practice the possible number of offspring will be limited and for all but a finite number of α the clock driving Y_α will never start. The meaning of the equation may be more obvious in the "infinitesimal form" given in Eq. (2.4) below.

For completeness we give a full proof of the existence and uniqueness of solutions to (2.1). The proof is similar to that for a fixed environment as considered without a detailed proof in ([9], Chap.6.4).

Theorem 2.1. *Assume*

$$\sum_{\alpha\in\tilde{\mathbb{Z}}_+^d} \alpha_j \int_0^t \Lambda_{\alpha+e_i}^{(i)}(s)\mathrm{d}s < \infty \text{ a.s. for all } t \geq 0 \text{ and each } i,j \in S. \tag{2.2}$$

Then for given $\mathbf{Z}(0) \in \mathbb{Z}_+^d$ the solution of Eq.(2.1) exists for all time and is unique a.s.

Proof. First of all, we will show the existence of a solution. Construct the solution by iteration as follows:

$$\begin{aligned} \mathbf{Z}^{(0)}(t) &= \mathbf{Z}(0), \\ \mathbf{Z}^{(n)}(t) &= \mathbf{Z}(0) + \sum_{\alpha\in\tilde{\mathbb{Z}}_+^d} \alpha Y_\alpha\left(\int_0^t \Lambda_\alpha(s)\cdot\mathbf{Z}^{(n-1)}(s)\mathrm{d}s\right), \text{ for } n \in \mathbb{N}. \end{aligned}$$

It is conventional to consider $\mathbf{0}$ as the absorbing state of $\{\mathbf{Z}^{(n)}(t)\}_{t\geq 0}$ for $n \in \mathbb{N}$.

Let $\mu(\mathrm{d}t) = \sum_\alpha \|\alpha\|_1 \sum_i \Lambda_{\alpha+e_i}^{(i)}(t)\mathrm{d}t$. Then $\mu[0,t] < \infty$ by (2.2). Let $\|\cdot\|_1$ denote the 1-norm of a vector. We claim that

$$\mathrm{E}\Big[\big\|\mathbf{Z}^{(n)}(t) - \mathbf{Z}^{(n-1)}(t)\big\|_1 \,\Big|\, \Lambda\Big] \leq \|\mathbf{Z}(0)\|_1 \frac{(\mu[0,t])^n}{n!}. \tag{2.3}$$

Indeed,

$$\begin{aligned} &\mathrm{E}\Big[\big\|\mathbf{Z}^{(n)}(t) - \mathbf{Z}^{(n-1)}(t)\big\|_1 \,\Big|\, \Lambda\Big] \\ &= \mathrm{E}\Big[\Big\|\sum_{\alpha\in\tilde{\mathbb{Z}}_+^d} \alpha\Big(Y_\alpha\Big(\int_0^t \Lambda_\alpha(s)\cdot\mathbf{Z}^{(n-1)}(s)\mathrm{d}s\Big) \\ &\qquad\qquad - Y_\alpha\Big(\int_0^t \Lambda_\alpha(s)\cdot\mathbf{Z}^{(n-2)}(s)\mathrm{d}s\Big)\Big)\Big\|_1 \,\Big|\, \Lambda\Big] \\ &\leq \int_0^t \Big(\sum_{\alpha\in\tilde{\mathbb{Z}}_+^d} \|\alpha\|_1 \sum_{i\in S} \Lambda_{\alpha+e_i}^{(i)}(s)\Big)\mathrm{E}\Big[\big\|\mathbf{Z}^{(n-1)}(s) - \mathbf{Z}^{(n-2)}(s)\big\|_1 \,\Big|\, \Lambda\Big]\mathrm{d}s \\ &= \int_0^t \mathrm{E}\Big[\big\|\mathbf{Z}^{(n-1)}(s_1) - \mathbf{Z}^{(n-2)}(s_1)\big\|_1 \,\Big|\, \Lambda\Big]\mu(\mathrm{d}s_1) \\ &\leq \int_0^t \int_0^{s_1} \cdots \int_0^{s_{n-1}} \|\mathbf{Z}(0)\|_1 \mu(\mathrm{d}s_n)\cdots\mu(\mathrm{d}s_2)\mu(\mathrm{d}s_1) \\ &= \|\mathbf{Z}(0)\|_1 \frac{(\mu[0,t])^n}{n!}. \end{aligned}$$

Let $\tilde{Y}_\alpha(t) = Y_\alpha(t) - t$. Then we have

$$\begin{aligned}
&\sup_{0\le t\le T}\left\|\mathbf{Z}^{(n)}(t) - \mathbf{Z}^{(n-1)}(t)\right\|_1 \\
&\le \int_0^T \Big\| \sum_{\alpha\in\tilde{\mathbb{Z}}_+^d} \alpha\Lambda_\alpha(s)\big(\mathbf{Z}^{(n-1)}(s) - \mathbf{Z}^{(n-2)}(s)\big)\Big\|_1 \mathrm{d}s \\
&\quad + \sup_{0\le t\le T}\Big\| \sum_{\alpha\in\tilde{\mathbb{Z}}_+^d} \alpha\Big(\tilde{Y}_\alpha\Big(\int_0^t \Lambda_\alpha(s)\cdot\mathbf{Z}^{(n-1)}(s)\mathrm{d}s\Big) \\
&\qquad\qquad -\tilde{Y}_\alpha\Big(\int_0^t \Lambda_\alpha(s)\cdot\mathbf{Z}^{(n-2)}(s)\mathrm{d}s\Big)\Big)\Big\|_1.
\end{aligned}$$

By Markov's inequality and the martingale property [16], it follows that

$$\begin{aligned}
&\mathrm{P}\Big[\sup_{0\le t\le T}\left\|\mathbf{Z}^{(n)}(t) - \mathbf{Z}^{(n-1)}(t)\right\|_1 > 2^{-n}\;\Big|\;\Lambda\Big] \\
&\le \mathrm{P}\Big[\int_0^T \Big\| \sum_{\alpha\in\tilde{\mathbb{Z}}_+^d} \alpha\Lambda_\alpha(s)\big(\mathbf{Z}^{(n-1)}(s) - \mathbf{Z}^{(n-2)}(s)\big)\Big\|_1 \mathrm{d}s > 2^{-n-1}\;\Big|\;\Lambda\Big] \\
&\quad +\mathrm{P}\Big[\sup_{0\le t\le T}\Big\| \sum_{\alpha\in\tilde{\mathbb{Z}}_+^d} \alpha\Big(\tilde{Y}_\alpha\Big(\int_0^t \Lambda_\alpha(s)\cdot\mathbf{Z}^{(n-1)}(s)\mathrm{d}s\Big) \\
&\qquad\qquad -\tilde{Y}_\alpha\Big(\int_0^t \Lambda_\alpha(s)\cdot\mathbf{Z}^{(n-2)}(s)\mathrm{d}s\Big)\Big)\Big\|_1 > 2^{-n-1}\;\Big|\;\Lambda\Big] \\
&\le 2^{n+1}\mathrm{E}\Big[\int_0^T \Big\| \sum_{\alpha\in\tilde{\mathbb{Z}}_+^d} \alpha\Lambda_\alpha(s)\big(\mathbf{Z}^{(n-1)}(s) - \mathbf{Z}^{(n-2)}(s)\big)\Big\|_1 \mathrm{d}s\;\Big|\;\Lambda\Big] \\
&\quad +2^{n+1}\mathrm{E}\Big[\Big\| \sum_{\alpha\in\tilde{\mathbb{Z}}_+^d} \alpha\Big(\tilde{Y}_\alpha\Big(\int_0^T \Lambda_\alpha(s)\cdot\mathbf{Z}^{(n-1)}(s)\mathrm{d}s\Big) \\
&\qquad\qquad -\tilde{Y}_\alpha\Big(\int_0^T \Lambda_\alpha(s)\cdot\mathbf{Z}^{(n-2)}(s)\mathrm{d}s\Big)\Big)\Big\|_1\;\Big|\;\Lambda\Big] \\
&\le 2^{n+1}(1+2)\int_0^T \sum_\alpha \|\alpha\|_1 \sum_i \Lambda^{(i)}_{\alpha+e_i}(s)\mathrm{E}\Big[\left\|\mathbf{Z}^{(n-1)}(s) - \mathbf{Z}^{(n-2)}(s)\right\|_1\;\Big|\;\Lambda\Big]\mathrm{d}s \\
&\le 6\|\mathbf{Z}(0)\|_1\frac{(2\mu[0,t])^n}{n!}.
\end{aligned}$$

By the Borel-Cantelli lemma [12], we get

$$\mathrm{P}\Big[\sup_{0\le t\le T}\left\|\mathbf{Z}^{(n)}(t) - \mathbf{Z}^{(n-1)}(t)\right\|_1 > 2^{-n} \text{ for infinitely many n}\;\Big|\;\Lambda\Big] = 0.$$

Therefore, $\mathbf{Z}^{(n)}(t,\bar{\omega})$ is uniformly convergent in $[0,T]$ for almost all $\bar{\omega}\in\Omega$. Let $\mathbf{Z}(t,\bar{\omega})$ denote the limit of the sequence $\mathbf{Z}^{(n)}(t,\bar{\omega})$. Then $\mathbf{Z}(t)$ satisfies Eq.(2.1). From (2.3) we obtain convergence of $\left\|\mathbf{Z}^{(n)}(t,\omega)\right\|_1$ for fixed $\omega\in\Omega_R$ in $L^1(\Omega_B)$ to $\|\mathbf{Z}(t,\omega)\|_1$. Hence we have $\mathrm{E}[\|\mathbf{Z}(t)\|_1 \mid \Lambda] < \infty$.

Next we will show the uniqueness of solutions of Eq.(2.1). Suppose there exist two integrable and measurable solutions $\mathbf{Z}$ and $\tilde{\mathbf{Z}}$ of Eq.(2.1) with given $\mathbf{Z}(0) = \tilde{\mathbf{Z}}(0)$. Then conditioned on Λ,

$$\begin{aligned}
&\mathrm{E}[\|\mathbf{Z}(t) - \tilde{\mathbf{Z}}(t)\|_1 \mid \Lambda] \\
&= \mathrm{E}\Big[\Big\| \sum_{\alpha \in \tilde{\mathbb{Z}}_+^d} \alpha\Big(Y_\alpha\Big(\int_0^t \Lambda_\alpha(s) \cdot \mathbf{Z}(s)\mathrm{d}s\Big) - Y_\alpha\Big(\int_0^t \Lambda_\alpha(s) \cdot \tilde{\mathbf{Z}}(s)\mathrm{d}s\Big)\Big)\Big\|_1 \Big| \Lambda\Big] \\
&\le \int_0^t \Big(\sum_{\alpha \in \tilde{\mathbb{Z}}_+^d} \|\alpha\|_1 \sum_{i \in S} \Lambda_{\alpha+e_i}^{(i)}(s)\Big)\mathrm{E}[\|\mathbf{Z}(s) - \tilde{\mathbf{Z}}(s)\|_1 \mid \Lambda]\mathrm{d}s.
\end{aligned}$$

Then by Gronwall's inequality [15], $\mathrm{P}\{\mathrm{E}[\|\mathbf{Z}(t) - \tilde{\mathbf{Z}}(t)\|_1 \mid \Lambda] = 0, \text{ for } t \ge 0\} = 1$. Hence $\mathrm{P}\{\mathbf{Z}(t) = \tilde{\mathbf{Z}}(t), \text{ for } t \ge 0\} = 1$, the uniqueness holds. □

Theorem 2.2. *The conditional transition probability of the process* $\mathbf{Z}(t)$ *in a time interval* $(t, t+\Delta t)$ *is*

$$\mathrm{P}\{\mathbf{Z}(t+\Delta t) - \mathbf{Z}(t) = \alpha \mid \mathcal{F}_t\} = \mathrm{E}\Big[\int_t^{t+\Delta t} \Lambda_\alpha(s) \cdot \mathbf{Z}(s)\mathrm{d}s \Big| \mathcal{F}_t\Big] + o(\Delta t), \tag{2.4}$$

where $\mathcal{F}_t := \sigma\{\mathbf{Z}(s) : 0 \le s \le t\}$.

Remark 2.3. Recall that $\Lambda_{\alpha+e_i}^{(i)}(t)\Delta t$ is the probability that a given individual of type i dies and is replaced by $\alpha + e_i$ offsprings in a time interval $(t, t+\Delta t)$. Eq.(2.4) implies the branching property which says that all individuals living at the same moment behave independently of one another when conditioned on the environment.

Proof. Let A denote the event

$$\Big\{Y_\alpha\left(\int_0^{t+\Delta t} \Lambda_\alpha(s) \cdot \mathbf{Z}(s)\mathrm{d}s\right) - Y_\alpha\left(\int_0^t \Lambda_\alpha(s) \cdot \mathbf{Z}(s)\mathrm{d}s\right) = 1\Big\}.$$

Then

$$\begin{aligned}
&\mathrm{P}\{\mathbf{Z}(t+\Delta t) - \mathbf{Z}(t) = \alpha \mid \mathcal{F}_t\} \\
&= \mathrm{P}\{A \mid \mathcal{F}_t\} \\
&= \mathrm{E}[\mathrm{P}[A \mid \mathcal{F}_{t+\Delta t}, \Lambda] \mid \mathcal{F}_t] \\
&= \mathrm{E}\Big[\int_t^{t+\Delta t} \Lambda_\alpha(s) \cdot \mathbf{Z}(s)\mathrm{d}s \Big| \mathcal{F}_t\Big] + o(\Delta t).
\end{aligned}$$

□

3. The Instability Property

We generalize the parallel mutation-reproduction model in [5] to one with a random environment. In this extended model, an individual of type i may, at each moment in continuous time, do one of three things: It may produce a copy of itself (at rate $\Lambda_{2e_i}^{(i)}$), it may die (at rate $\Lambda_{\mathbf{0}}^{(i)}$), or it may mutate to type j ($j \ne i$) (at rate $\Lambda^{(i)}_{e_j}$). For simplicity, we consider only two types, i.e., $S = \{1, 2\}$. However, a generalization to the multitype case is not difficult.

This will be a special case of a two-type Markov branching process in a random environment. The branching process is still denoted by $\{\mathbf{Z}(t)\}_{t\geq 0}$. Write $\mathcal{I}_1 = \{e_1, -e_1, e_2 - e_1\}$ and $\mathcal{I}_2 = \{e_2, -e_2, e_1 - e_2\}$. For all $\alpha \in \mathcal{I}_i$ and $i \in S$, assume $\Lambda^{(i)}_{\alpha+e_i}$ is controlled by the environment stochastic process η and we can write $\Lambda^{(i)}_{\alpha+e_i}(t,\omega)$ as $\Lambda^{(i)}_{\alpha+e_i}(\eta(t,\omega))$. Assume $\sum_{\alpha\in\mathcal{I}_i} \alpha_j \int_0^t \Lambda^{(i)}_{\alpha+e_i}(s)\mathrm{d}s < \infty$ a.s. for all $t \geq 0$ and $i, j \in S$. Then Theorem 2.1 shows the existence of such a process. We will call $\{\mathbf{Z}(t)\}_{t\geq 0}$ a two-type parallel mutation-reproduction Markov branching process in the random environment $\{\eta(t)\}_{t\geq 0}$.

We want to show an instability property of $\{\mathbf{Z}(t)\}_{t\geq 0}$ as in [8] which we follow closely. For this purpose, we make a further assumption on the random environment (named *Environmental Assumption*): *$\{\eta(t)\}_{t\geq 0}$ is an irreducible, positive recurrent, Markov chain in continuous time on a countable state space $\mathcal{Y}$ with jump times $\tau_n \uparrow +\infty$, $n \geq 0$.*

Take $\tau_0 = 0$ and let the infinitesimal parameters be $\{q_{xy}\}$, $x, y \in \mathcal{Y}$. Write $q_y = 1/\mathrm{E}_y\tau_1$ and note positive recurrence implies that $\mathrm{E}_y\tau_1 < \infty$ and $q_y > 0$. The evolution of the process $\{\mathbf{Z}(t)\}_{t\geq 0}$ can also be described as follows: in the time interval $[\tau_{n-1}, \tau_n)$, $n \geq 1$, $\{\mathbf{Z}(t)\}_{t\geq 0}$ evolves as a two-type parallel mutation-reproduction Markov branching process in a fixed environment with associated jump times $T_l(n)$, $1 \leq l \leq k_n$. Set $T_0(n) = \tau_{n-1}$, $n \geq 1$. So, the environmental process $\{\eta(t)\}_{t\geq 0}$ jumps at times $T_0(n)$, and the process $\{\mathbf{Z}(t)\}_{t\geq 0}$ jumps at times $T_l(n)$, $1 \leq l \leq k_n$. This gives a sequence $\{T_l(n),\ 0 \leq l \leq k_n,\ n \geq 1\}$ of exponentially distributed random variables such that

$$\begin{aligned} 0 = \tau_0 = T_0(1) < T_1(1) < \cdots < T_{k_1}(1) \\ < \tau_1 = T_0(2) < T_1(2) < \cdots < T_{k_2}(2) < \cdots, \end{aligned}$$

with obvious modifications when $k_n = 0$. For $r \geq 1$, let T_r denote the rth element of this sequence. Then for a fixed r, and for a given realization of $\{(\eta(t), \mathbf{Z}(t))\}_{t\geq 0}$, there exist unique n and l such that

$$T_r = T_l(n), \text{ with } 0 \leq l \leq k_n. \tag{3.1}$$

Now we consider the embedded chain $\{(\tilde{\eta}_n, \tilde{\mathbf{Z}}_n)\}_{n\in\mathbb{N}_0}$ of the Markov process $\{(\eta(t), \mathbf{Z}(t))\}_{t\geq 0}$, defined by

$$\{(\tilde{\eta}_n, \tilde{\mathbf{Z}}_n)\}_{n\in\mathbb{N}_0} = \{(\eta(\tau_n), \mathbf{Z}(\tau_n))\}_{n\in\mathbb{N}_0}.$$

It is important to note that $\{(\tilde{\eta}_n, \tilde{\mathbf{Z}}_n)\}_{n\in\mathbb{N}_0}$ satisfy the following relation:

$$\begin{aligned} &\mathrm{P}_{(y,\mathbf{z})}\{\tilde{\mathbf{Z}}_{n+1} \in B \mid \tilde{\eta}_0, \tilde{\eta}_1, \cdots; \tilde{\mathbf{Z}}_0, \tilde{\mathbf{Z}}_1, \cdots, \tilde{\mathbf{Z}}_n\} \\ = \ &\mathrm{P}_{(y,\mathbf{z})}\{\tilde{\mathbf{Z}}_{n+1} \in B \mid \tilde{\eta}_n, \tilde{\mathbf{Z}}_n\}, \text{ for every } (y, \mathbf{z}) \in \mathcal{Y} \times \mathbb{Z}_+^2 \text{ and } B \subseteq \mathbb{Z}_+^2. \end{aligned} \tag{3.2}$$

Then (3.2) together with the fact that $\{\tilde{\eta}_n\}_{n\in\mathbb{N}_0}$ is a Markov chain implies that $\{(\tilde{\eta}_n, \tilde{\mathbf{Z}}_n)\}_{n\in\mathbb{N}_0}$ is Markov.

Cogburn studied processes $\{(\eta_n, \mathbf{Z}_n)\}_{n\in\mathbb{N}_0}$ satisfying the relation (3.2) and with $\{\eta_n\}_{n\in\mathbb{N}_0}$ Markov and called the marginal process $\{\mathbf{Z}_n\}_{n\in\mathbb{N}_0}$ a Markov chain in a random environment $\{\eta_n\}_{n\in\mathbb{N}_0}$ [7]. An important and useful concept in the study of these processes is the notion of a proper Markov chain in a random environment. Recall $\{\mathbf{Z}_n\}_{n\in\mathbb{N}_0}$ is called proper if for $\mathbf{z}\in\mathbb{Z}_+^2$, whenever

$$\sup_{y\in\mathcal{Y}} \mathrm{P}_{(y,\mathbf{z})}\{\mathbf{Z}_n=\mathbf{z} \text{ i.o.}\}>0,$$

where $\{\mathbf{Z}_n=\mathbf{z} \text{ i.o.}\}$ means that the event $\{\mathbf{Z}_n=\mathbf{z}\}$ happens infinitely often, then $(y,\mathbf{z})$ is recurrent for some $y\in\mathcal{Y}$ for the Markov chain $\{(\eta_n,\mathbf{Z}_n)\}_{n\in\mathbb{N}_0}$.

Remark 3.1. (*Cogburn and Torrez* [8]) If a Markov chain in a random environment, $\{\mathbf{Z}_n\}_{n\in\mathbb{N}_0}$, is proper, and states of $\mathcal{Y}\times(\mathbb{Z}_+^2\backslash\{\mathbf{0}\})$ communicate (that two states communicate means that the former is accessible from the latter and the latter is also accessible from the former) and lead to $\mathcal{Y}\times\{\mathbf{0}\}$ (that means any state of $\mathcal{Y}\times(\mathbb{Z}_+^2\backslash\{\mathbf{0}\})$ can reach the absorbing states $\mathcal{Y}\times\{\mathbf{0}\}$ with a positive probability), then necessarily $(y,\mathbf{z})$ is transient and $\mathrm{P}_{(y,\mathbf{z})}\{\mathbf{Z}_n=\mathbf{z}' \text{ i.o.}\}=0$ for all $(y,\mathbf{z})\in\mathcal{Y}\times\mathbb{Z}_+^2$ and $\mathbf{z}'\neq\mathbf{0}$ and hence

$$\mathrm{P}_{(y,\mathbf{z})}\{\lim_{n\to\infty}\|\mathbf{Z}_n\|_1= \ 0 \text{ or } \infty\}=1, \text{for every } (y,\mathbf{z})\in\mathcal{Y}\times\mathbb{Z}_+^2.$$

In this section, our main result (Theorem 3.4) follows by an application of a result (Theorem 3.3) due to Cogburn. Before stating Theorems 3.3 and 3.4, recall the definition of uniform $\varphi-$recurrence given in [17].

Definition 3.2. Let φ be a $\sigma-$finite, nontrivial measure on $(\mathcal{Y},\mathcal{B})$. A Markov chain $\{\eta_n\}_{n\in\mathbb{N}_0}$ on $(\mathcal{Y},\mathcal{B})$ is *uniformly $\varphi-$recurrent* if

$$\sup_{y\in\mathcal{Y}} \mathrm{P}_y\{\tau_A>n\}\to 0 \text{ as } n\to\infty,$$

where τ_A denotes the first entrance time of $\{\eta_n\}_{n\in\mathbb{N}_0}$ to a set $A\in\mathcal{B}$, whenever $\varphi(A)>0$.

Theorem 3.3 will allow us to assert that the Markov chain in a random environment, $\{\mathbf{Z}(\tau_n)\}_{n\in\mathbb{N}_0}$, is proper. For the proof of Theorem 3.3 see Theorem 2.1 in [7].

Theorem 3.3. **(Cogburn** [7]**)** *Let $\{\mathbf{Z}_n\}_{n\in\mathbb{N}_0}$ be a Markov chain in a random environment $\{\eta_n\}_{n\in\mathbb{N}_0}$. Let $\mathrm{P}^{(y)}\{\mathbf{z},\mathbf{z}'\}$ denote the transition probability of $\{\mathbf{Z}_n\}_{n\in\mathbb{N}_0}$ in the yth environment. Suppose that*

(a): *for each $\mathbf{z}\in\mathbb{Z}_+^2$ there exists a finite set $B_{\mathbf{z}}\subseteq\mathbb{Z}_+^2$ such that*

$$\inf_{y\in\mathcal{Y}} \mathrm{P}^{(y)}\{\mathbf{z},B_{\mathbf{z}}\}>0;$$

(b): *the Markov chain $\{\eta_n\}_{n\in\mathbb{N}_0}$ is uniformly $\varphi-$recurrent.*

Then $\{\mathbf{Z}_n\}_{n\in\mathbb{N}_0}$ is a proper Markov chain in a random environment.

We now turn to our main result. In the statement, assumption (a) gives conditions on infinitesimal parameters of our process which together with assumption (b) will ensure the conditions of Theorem 3.3 are satisfied. Combined with assumption (c), this ensures, via Remark 3.1, that all non-zero states are transient.

Theorem 3.4. *Let $\{\mathbf{Z}(t)\}_{t\geq 0}$ be a two-type parallel mutation-reproduction Markov branching process in a random environment $\{\eta(t)\}_{t\geq 0}$ satisfying the Environmental Assumption above. Suppose that*

(a): *for each* $\mathbf{z} \in \mathbb{Z}_+^2$ *there exists a positive integer* $n_{\mathbf{z}} > \|\mathbf{z}\|_1$ *such that*

$$\inf_{y \in \mathcal{Y}} m_{\mathbf{z}}^{(y)} / q_y > 0,$$

where $m_{\mathbf{z}}^{(y)} = \sum_{k=\|\mathbf{z}\|_1}^{n_{\mathbf{z}}} \sigma_k^{(y)}$ *with*

$$\sigma_k^{(y)} = \sum_{\{(z_1,z_2)^\top \in \mathbb{Z}_+^2 : z_1+z_2=k\}} (z_1 \Lambda_{(2,0)^\top}^{(1)}(y) + z_2 \Lambda_{(0,2)^\top}^{(2)}(y));$$

(b): *the embedded chain* $\{\eta(\tau_n)\}_{n\in\mathbb{N}_0}$ *is uniformly* $\varphi-$*recurrent;*

(c): *states of* $\mathcal{Y} \times (\mathbb{Z}_+^2 \backslash \{\mathbf{0}\})$ *communicate and lead to* $\mathcal{Y} \times \{\mathbf{0}\}$.

Then $\mathrm{P}_{(y,\mathbf{z})}\{\lim_{t\to\infty} \|\mathbf{Z}(t)\|_1 = \ 0 \text{ or } \infty\} = 1$, *for every* $(y, \mathbf{z}) \in \mathcal{Y} \times \mathbb{Z}_+^2$.

Proof. This theorem is a generalization of Theorem 2.2 in [8] to the multitype situation, and its proof closely follows the pattern of the proof in [8].

First of all, we want to show that the embedded process $\{\mathbf{Z}(\tau_n)\}_{n\in\mathbb{N}_0}$ is proper by Theorem 3.3. Set $B_{\mathbf{z}} = \{\mathbf{x} \in \mathbb{Z}_+^2 : \|\mathbf{x}\|_1 \le n_{\mathbf{z}}\}$. We will show

$$\inf_{y\in\mathcal{Y}} \mathrm{P}^{(y)}\{\mathbf{z}, B_{\mathbf{z}}\} > 0, \tag{3.3}$$

for each $\mathbf{z} \in \mathbb{Z}_+^2$. It is enough to show that if T is the first-passage time to a state whose norm is $n_{\mathbf{z}} + 1$, then $\inf_{y\in\mathcal{Y}} \mathrm{P}_{(y,\mathbf{z})}\{T > \tau_y\} > 0$, where τ_y is the first jump time of $\{\eta(t)\}_{t\ge 0}$ with initial state y.

Note that T is stochastically larger than the sum of the independent first-passage times of $\mathbf{Z}(t)$ to level $k+1$ starting at a state in level k, for $\|\mathbf{z}\|_1 \le k \le n_{\mathbf{z}}$. Setting $N = n_{\mathbf{z}} + 1 - \|\mathbf{z}\|_1$ it follows that

$$\begin{aligned} \mathrm{P}_{(y,\mathbf{z})}\{T > \tau_y\} &= \int_0^\infty \mathrm{P}_{(y,\mathbf{z})}\{T > t\} q_y e^{-q_y t} dt \\ &\ge q_y \int_0^\infty \exp\{-(q_y + (m_{\mathbf{z}}^{(y)}/N))t\} dt \\ &= N q_y / (N q_y + m_{\mathbf{z}}^{(y)}). \end{aligned} \tag{3.4}$$

Assumption (a) implies that the infimum over $y \in \mathcal{Y}$ of the right hand side of (3.4) is positive and therefore (3.3) follows. Together with assumption (b), we obtain that $\{\mathbf{Z}(\tau_n)\}_{n\in\mathbb{N}_0}$ is proper by Theorem 3.3.

By assumption (c) and the fact that $\mathbf{0}$ is an absorbing state in each environment, we may conclude from Remark 3.1 that the following holds:

$$\mathrm{P}_{(y,\mathbf{z})}\{\lim_{n\to\infty} \|\mathbf{Z}(\tau_n)\|_1 = \ 0 \text{ or } \infty\} = 1, \text{ for every } (y,\mathbf{z}) \in \mathcal{Y} \times \mathbb{Z}_+^2. \tag{3.5}$$

We will show that the conclusion above holds for $\{\mathbf{Z}(t)\}_{t\ge 0}$. We have shown that

$$\inf_{y\in\mathcal{Y}} \mathrm{P}_{(y,\mathbf{z})}\{\|\mathbf{Z}(\tau_1)\|_1 \le n_{\mathbf{z}}\} = \inf_{y\in\mathcal{Y}} \mathrm{P}_{(y,\mathbf{z})}\{T > \tau_y\} > 0.$$

Then there exists $\varepsilon > 0$ such that

$$\inf_{y\in\mathcal{Y}} \mathrm{P}_{(y,\mathbf{z})}\{\|\mathbf{Z}(\tau_1)\|_1 \le n_{\mathbf{z}}\} \ge \varepsilon.$$

For $\mathbf{z}' \in \mathbb{Z}_+^2 \backslash \{\mathbf{0}\}$, the strong Markov property yields

$$\mathrm{P}_{(y,\mathbf{z})}\{\|\mathbf{Z}(\tau_n)\|_1 \le n_{\mathbf{z}'} \mid \eta(T_l(n)) = y', \mathbf{Z}(T_l(n)) = \mathbf{z}'\} \ge \varepsilon, \text{ for } y' \in \mathcal{Y}.$$

Then it follows that

$$\mathrm{P}_{(y,\mathbf{z})}\{\|\mathbf{Z}(\tau_n)\|_1 \le n_{\mathbf{z}'} \mid \mathbf{Z}(T_l(n)) = \mathbf{z}'\} \ge \varepsilon.$$

Recall the relation of the $T_l(n)'$s and T_n's in (3.1). Hence

$$\mathrm{P}_{(y,\mathbf{z})}\{\|\mathbf{Z}(\tau_n)\|_1 \le n_{\mathbf{z}'} \text{ i.o.}\} \ge \varepsilon \mathrm{P}_{(y,\mathbf{z})}\{\mathbf{Z}(T_n) = \mathbf{z}' \text{ i.o.}\}. \tag{3.6}$$

Note that for every $(y, \mathbf{z}) \in \mathcal{Y} \times \mathbb{Z}_+^2$,

$$\mathrm{P}_{(y,\mathbf{z})}\{\lim_{n\to\infty} \|\mathbf{Z}(\tau_n)\|_1 = 0\} = \mathrm{P}_{(y,\mathbf{z})}\{\lim_{n\to\infty} \|\mathbf{Z}(T_n)\|_1 = 0\}. \tag{3.7}$$

The conclusion of the theorem follows by equations (3.5), (3.6) and (3.7) since the asymptotic behavior of $\{\mathbf{Z}(t)\}_{t\ge 0}$ is the same as $\{\mathbf{Z}(T_n)\}_{n\in\mathbb{N}}$. □

Example 3.5. Let the environment process be $\eta(t) = (-1)^{\xi(t)}$, $t \ge 0$, where $\{\xi(t)\}_{t\ge 0}$ is a standard Poisson process defined on $\mathbb{Z}_+$. For fixed integers $n > 1$ and $m > 1$, set the splitting intensities of the branching process as follows: $\Lambda^{(1)}_{(0,0)^\top}(t) \equiv 1$, $\Lambda^{(1)}_{(2,0)^\top}(t) = 1 + n^{-1/2}\eta(t)$, $\Lambda^{(1)}_{(0,1)^\top}(t) = n^{-1}$, $\Lambda^{(2)}_{(0,0)^\top}(t) \equiv 1$, $\Lambda^{(2)}_{(0,2)^\top}(t) = 1 + m^{-1/2}\eta(t)$, $\Lambda^{(2)}_{(1,0)^\top}(t) = m^{-1}$. This is a modification of a one-type example described in Chap.9.3 of [9] in a different context. It is easy to verify that the example satisfies assumptions of Theorem 3.4, therefore the instability holds.

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References

1. Athreya, K. B. and Karlin, S.: Branching processes in random environments, *PAMS* **76** (1970) 865–870.
2. Athreya, K. B. and Karlin, S.: On branching processes in random environments: I. Extinction probability, *Ann. Math. Statist.* **42** (1971) 1499–1520.
3. Athreya, K. B. and Karlin, S.: On branching processes in random environments: II. Limit theorems, *Ann. Math. Statist.* **42** (1971) 1843–1858.
4. Athreya, K. B. and Ney, P. E.: *Branching Processes*, Springer Verlag, Berlin, 1972.
5. Baake, E. and Georgii, H. O.: Mutation, selection, and ancestry in branching models: a variational approach, *J. Math. Biol.* **54** (2007) 257–303.
6. Benaïm, M. and Schreiber, S. J.: Persistence of structured populations in random environments, *Theor Popul Biol.* **76** (2009) 19–34.
7. Cogburn, R: Markov chains in random environments: the case of Markovian environments, *Ann. Probab.* **8** (1980) 908–916.
8. Cogburn, R. and Torrez, W. C.: Birth and death processes with random environments in continuous time, *J. Appl. Probab.* **18** (1981) 19–30.
9. Ethier, S. N. and Kurtz, T. G.: *Markov Processes: Characterization and Convergence*, John Wiley & Sons, New York, 1986.

10. Haccou, P. and Jagers, P. and Vatutin, V. A.: *Branching Processes: Variation, Growth, and Extinction of Populations*, Cambridge University Press, Cambridge, 2005.
11. Harris, T. E.: *The Theory of Branching Processes*, Springer, Berlin, 1963.
12. Kallenberg, O.: *Foundation of Modern Probability*, Springer, Berlin, 2001.
13. Keiding, N.: Extinction and exponential growth in random environments, *Theor Popul Biol.* **8** (1975) 49–63.
14. Kimmel, M. and Axelrod, D. E.: *Branching Processes in Biology*, Springer, 2002.
15. Mao, X. R. and Yuan, C. G.: *Stochastic Differential Equations with Markovian Switching*, Imperial College Press, 2006.
16. Øksendal, B.: *Stochastic Differential Equations: An Introduction with Applications*, Springer Verlag, Heidelberg New York, 2003.
17. Torrez, W. C.: The birth and death chain in a random environment: instability and extinction theorems, *Ann. Probab.* **6** (1978) 1026–1043.
18. Wang, Y.: Continuous approximation for parallel mutation-reproduction processes in random environments, *In preparation*.

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