TWO-SEX BRANCHING PROCESSES WITH OFFSPRING AND MATING IN A RANDOM ENVIRONMENT

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Abstract

We introduce a class of discrete-time two-sex branching processes where the offspring probability distribution and the mating function are governed by an environmental process. It is assumed that the environmental process is formed by independent but not necessarily identically distributed random vectors. For such a class, we determine some relationships among the probability generating functions involved in the mathematical model and derive expressions for the main moments. Also, by considering different probabilistic approaches we establish several results concerning the extinction probability. A simulated example is presented as an illustration.

Keywords: Branching process; two-sex process; random environment process; extinction probability

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1. Introduction

Mathematical models in which individuals may be replaced by others of a similar or different type are now being developed. It is an active research area of both theoretical interest and applicability to such fields as biology, demography, ecology, epidemiology, genetics, medicine, population dynamics, and physics. One may cite, for example, the monographs by Jagers (1975), Kimmel and Axelrod (2002), Pakes (2003), and Haccou *et al.* (2005), which include practical applications to cell kinetics, cell biology, chemotherapy, gene amplification, human evolution, and molecular biology.

In particular, it is our purpose to model the probabilistic evolution of populations where females and males coexist and form couples (female–male). Several classes of discrete-time two-sex (bisexual) branching processes have been studied, including the bisexual Galton–Watson process (see Alsmeyer and Rösler (1996), (2002), Bagley (1986), Bruss (1984), Daley (1968), and Daley *et al.* (1986)); processes with immigration (see González *et al.* (2000), (2001), and Ma and Xing (2006)); in varying environments (see Molina *et al.* (2003), (2004a)); and processes depending on the number of couples in the population (see Molina *et al.* (2002), (2004b), (2006), and Xing and Wang (2005)). We refer the reader to Hull (2003) or Haccou *et al.* (2005, pp. 43–46, 135–145, 177–179) for surveys of two-sex branching processes. Also, a general class of continuous-time two-sex branching processes was introduced in Molina and Yanev (2003).

It can be stated that significant efforts have been made regarding random environment models with asexual reproduction (see, e.g. Agresti (1975), Holzheimer (1984), Smith and Wilkinson (1969), and Yanev and Yanev (1990)). Now similar efforts should be made to develop a branching process with a random environment where reproduction is bisexual. So, in this work we introduce a class of two-sex branching processes with offspring probability distribution and mating function dependent on a random environmental process.

The paper is organized as follows. In Section 2, the probability model is described formally and interpreted intuitively. A simulated example is presented by way of illustration. Section 3 is devoted to determining some relationships among the probability generating functions involved in the mathematical model, deducing expressions for the main moments. Finally, in Section 4, several results concerning its extinction probability are established by considering different probabilistic approaches.

2. The two-sex model

On a probability space $(\Omega, \mathcal{F}, \mathrm{P})$ we introduce the two-sex branching process with offspring and mating in a random environment as the two-type sequence $\{(F_n, M_n)\}_{n \geq 1}$ defined in the form

$$(F_{n+1}, M_{n+1}) = \sum_{i=1}^{Z_n} (f_{n,i;\theta_n}, m_{n,i;\theta_n}), \qquad Z_{n+1} = L_{\eta_n}(F_{n+1}, M_{n+1}), \qquad n = 0, 1, \ldots,$$
(2.1)

where the empty sum is considered to be $(0, 0)$. The random vector (F_{n+1}, M_{n+1}) represents the number of females and males in the $(n + 1)$th generation. These females and males form Z_{n+1} couples. Initially, we assume that there is a positive number, N_0, of couples in the population, i.e. $Z_0 = N_0$.

The sequence $\{(\theta_n, \eta_n)\}_{n \geq 0}$ represents an environmental process consisting of independent but not necessarily identically distributed random vectors (θ_n, η_n) defined on $(\Omega, \mathcal{F}, \mathrm{P})$ and taking values in a certain space $\mathscr{S}$. Let $\mathbb{Z}^+$ be the set of nonnegative integers. If, for any $n \in \mathbb{Z}^+$, there exists (θ, η) in $\mathscr{S}$ such that $(\theta_n, \eta_n) = (\theta, \eta)$ then the following statements hold.

(a) $(f_{n,i;\theta}, m_{n,i;\theta})$, $i = 1, \ldots, Z_n$, are independent and identically distributed nonnegative random vectors on $(\Omega, \mathcal{F}, \mathrm{P})$. Intuitively, $(f_{n,i;\theta}, m_{n,i;\theta})$ represents the number of females and males descending from the ith couple of the nth generation, assuming that the environmental variable θ_n has taken the value θ. Its probability law is referred to as the offspring distribution when $\theta_n = \theta$.

(b) L_η is the function which governs the mating between females and males. It is defined on $\mathbb{R}^+ \times \mathbb{R}^+$ and takes values in $\mathbb{R}^+$, where $\mathbb{R}^+$ is the set of nonnegative real numbers. It is assumed to be nondecreasing in each argument, integer valued on the integers, and such that $L_\eta(x, 0) = L_\eta(0, y) = 0$, $x, y \in \mathbb{R}^+$.

The process $\{(F_n, M_n)\}_{n \geq 1}$ may be interpreted as a branching model developing in an environment which changes stochastically in time and which affects both the reproductive behaviour and the mating between females and males. In addition to its theoretical interest, this model also has clear practical implications, especially in population dynamics. For certain sexually reproducing animal populations, it is reasonable to assume that behaviour is affected by such environmental factors as weather, food supply, fertility parameters, and so on. For example, in making policy decisions as to whether to introduce or reintroduce certain animal species into an

environment, this class of process may provide appropriate mathematical models with which to describe the probabilistic behaviour of the population. Indeed, the motivation behind processes of the type presented in (2.1) is the interest in developing two-sex models for such phenomena. When the random vectors (θ_n, η_n) do not change with n, i.e. they have the same probability distribution for all n, the process defined in (2.1) reduces to the bisexual Galton–Watson process introduced in Daley (1968). This process has received much attention in the branching process literature (see, e.g. the survey by Hull (2003)).

Example 2.1. By way of illustration, let us consider a two-sex branching process in a random environment (2.1), in which the following statements hold.

(a) The environmental sequence $\{(\theta_n, \eta_n)\}_{n \geq 0}$ is such that θ_n and η_n are independent random variables for each n. We assume that θ_n has a beta distribution with parameters a_n and b_n, and η_n has an exponential distribution with mean λ_n^{-1}, where

$$a_n = (n+1)(n+2)^{-1}, \qquad b_n = (2n+1)(n+2)^{-1}, \quad \text{and} \quad \lambda_n = (5n+1)(n+1)^{-1}.$$

It follows that the joint probability density function of (θ_n, η_n) is given by

$$f_{(\theta_n, \eta_n)}(\theta, \eta) = \frac{\Gamma(a_n + b_n)}{\Gamma(a_n)\Gamma(b_n)} \theta^{a_n - 1}(1 - \theta)^{b_n - 1}\lambda_n e^{-\lambda_n \eta}, \qquad \theta \in (0, 1), \ \eta \in (0, \infty).$$

(Recall that, for $c > 0$, $\Gamma(c) = \int_0^\infty x^{c-1}e^{-x}\,dx$.)

(b) If $\theta_n = \theta$ for some $\theta \in (0, 1)$ then, independently of n, we assume as offspring probability law the trinomial distribution

$$P(f_{n,1;\theta} = k, \ m_{n,1;\theta} = j) = \frac{10!}{k!\,j!\,(10 - k - j)!}(0.9\theta)^k(0.9(1 - \theta))^j(0.1)^{10-k-j},$$

where k and j are nonnegative integers such that $k + j \leq 10$.

(c) If $\eta_n = \eta$ for some $\eta \in (0, \infty)$ then we assume that the mating between females and males is governed by the function

$$L_\eta(x, y) = \min\{x, \lfloor 3y\eta(1 + \eta)^{-1}\rfloor\}, \qquad x, y \in \mathbb{R}^+,$$

where $\lfloor z \rfloor$ denotes the integer part of z.

Starting with $N_0 = 35$ couples in the population, we simulated 20 generations of this process. The observed values of the environmental variables θ_n and η_n are shown in Figure 1. Graphics in Figure 1 reflect the fact that

$$\lim_{n \to \infty} E[\theta_n] = \lim_{n \to \infty} a_n(a_n + b_n)^{-1} = \tfrac{1}{3} \quad \text{and} \quad \lim_{n \to \infty} E[\eta_n] = \lim_{n \to \infty} \lambda_n^{-1} = 0.2.$$

On the other hand, the obtained values of females, males, and couples are shown in Figure 2. Note that, for the particular sample path observed, the process does not survive. The extinction problem will be considered in Section 4.
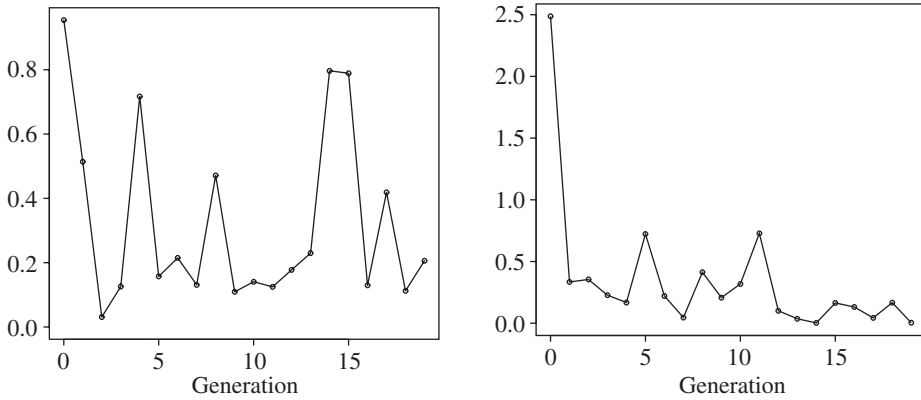
FIGURE 1: The observed values of the environmental variables θ_n (*left*) and η_n (*right*) for generations $n = 0, \ldots, 19$.
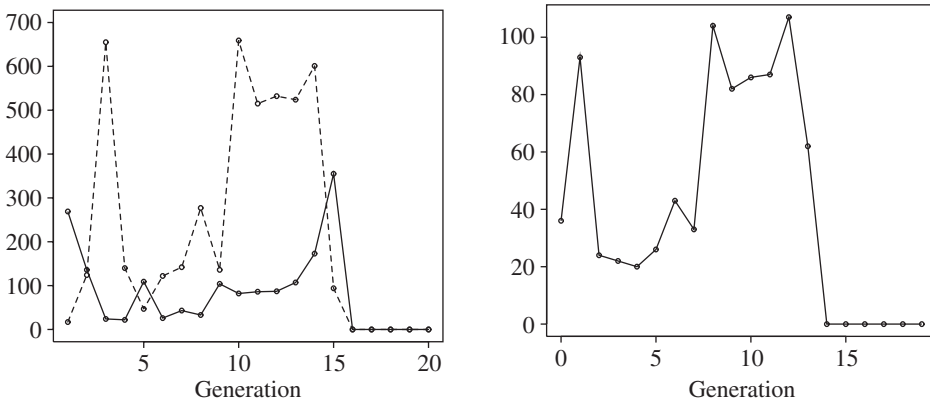

FIGURE 2: *Left*: the observed values of the numbers of females (*solid line*) and males (*dashed line*), i.e. (F_n, M_n), $n = 1, \ldots, 20$. *Right*: the observed value of the number of couples, i.e. Z_n, $n = 0, \ldots, 19$.

3. Probability generating functions

For $n \in \mathbb{Z}^+$ and $s_1, s_2 \in [0, 1]$, let

$$h_{n+1}(s_1, s_2) = \mathrm{E}[s_1^{F_{n+1}} s_2^{M_{n+1}}], \qquad g_n(s) = \mathrm{E}[s^{Z_n}], \quad \text{and} \quad \varphi_{n;\theta}(s_1, s_2) = \mathrm{E}[s_1^{f_{n,1;\theta}} s_2^{m_{n,1;\theta}}]$$

be the probability generating functions of (F_{n+1}, M_{n+1}), Z_n, and $(f_{n,1;\theta}, m_{n,1;\theta})$, respectively.

Proposition 3.1. *For $n \in \mathbb{Z}^+$,*

$$h_{n+1}(s_1, s_2) = \int_{\Theta_n} g_n(\varphi_{n;\theta}(s_1, s_2)) \, \mathrm{d}F_{\theta_n}(\theta), \qquad s_1, s_2 \in [0, 1],$$

where Θ_n denotes the set on which θ_n takes values and F_{θ_n} is the distribution function of θ_n.

Proof. Let $\mathcal{F}_n = \sigma(Z_0, \theta_0, \ldots, Z_n, \theta_n)$ be the σ-algebra generated by the variables $Z_0, \theta_0, \ldots, Z_n, \theta_n$. Then, for $n \in \mathbb{Z}^+$,

$$
\begin{aligned}
h_{n+1}(s_1, s_2) &= \mathrm{E}[\mathrm{E}[s_1^{F_{n+1}} s_2^{M_{n+1}} \mid \mathcal{F}_n]] \\
&= \int_{\Theta_n} \sum_{k=0}^{\infty} \mathrm{E}[s_1^{\sum_{i=1}^{k} f_{n,i;\theta}} s_2^{\sum_{i=1}^{k} m_{n,i;\theta}}] \, \mathrm{P}(Z_n = k) \, \mathrm{d}F_{\theta_n}(\theta) \\
&= \int_{\Theta_n} \sum_{k=0}^{\infty} (\mathrm{E}[s_1^{f_{n,1;\theta}} s_2^{m_{n,1;\theta}}])^k \, \mathrm{P}(Z_n = k) \, \mathrm{d}F_{\theta_n}(\theta) \\
&= \int_{\Theta_n} g_n(\varphi_{n;\theta}(s_1, s_2)) \, \mathrm{d}F_{\theta_n}(\theta), \qquad s_1, s_2 \in [0, 1].
\end{aligned}
$$

Using the notation $\mu_{n;\theta} = \mathrm{E}[(f_{n,1;\theta}, m_{n,1;\theta})]$ and $\Delta_{n;\theta} = \mathrm{cov}[(f_{n,1;\theta}, m_{n,1;\theta})]$ for the mean vector and the covariance matrix of the offspring distribution when $\theta_n = \theta$, respectively, from Proposition 3.1 we find by straightforward calculation the following expressions for the mean vector and the covariance matrix of (F_{n+1}, M_{n+1}), $n \in \mathbb{Z}^+$:

$$
\mathrm{E}[(F_{n+1}, M_{n+1})] = \mathrm{E}[Z_n] \, \mathrm{E}[\mu_{n;\theta_n}],
$$
$$
\mathrm{cov}[(F_{n+1}, M_{n+1})] = \mathrm{E}[Z_n] \, \mathrm{E}[\Delta_{n;\theta_n}] + \mathrm{var}[Z_n](\mathrm{E}[\mu_{n;\theta_n}])^{\top} \mathrm{E}[\mu_{n;\theta_n}],
$$

where $(\mathrm{E}[\mu_{n;\theta_n}])^{\top}$ denotes the transpose of the vector $\mathrm{E}[\mu_{n;\theta_n}]$.

Remark 3.1. We shall henceforth assume that all the mating functions L_η are superadditive, i.e. that they satisfy

$$
L_\eta(x_1 + x_2, y_1 + y_2) \geq L_\eta(x_1, y_1) + L_\eta(x_2, y_2), \qquad x_i, y_i \in \mathbb{R}^+, \, i = 1, 2.
$$

Superadditivity expresses the intuitive notion that $x_1 + x_2$ females and $y_1 + y_2$ males coexisting together will form a number of couples that is at least as great as the total number of couples formed by x_1 females and y_1 males, and x_2 females and y_2 males, living separately. This is not a severe constraint, since most mating functions considered in two-sex branching process theory are superadditive (see, e.g. Hull (1982) or Daley *et al.* (1986)).

Note that if $(\theta_n, \eta_n) = (\theta, \eta)$ then the variable $L_\eta(f_{n,1;\theta}, m_{n,1;\theta})$ represents the number of matings originated from the offspring of a couple in the nth generation. Let $\zeta_{n;(\theta,\eta)}(s) = \mathrm{E}[s^{L_\eta(f_{n,1;\theta}, m_{n,1;\theta})}]$, $s \in [0, 1]$, be its probability generating function. Since $Z_0 = N_0$, we have $g_0(s) = s^{N_0}$, $s \in [0, 1]$. We now provide upper and lower bounds for $g_{n+1}(s)$, $n \in \mathbb{Z}^+$.

Proposition 3.2. *For $n \in \mathbb{Z}^+$,*

$$
g_{n+1}(s) \leq \int_{\mathcal{S}} g_n(\zeta_{n;(\theta,\eta)}(s)) \, \mathrm{d}F_{(\theta_n,\eta_n)}(\theta, \eta), \qquad s \in [0, 1],
$$

where $F_{(\theta_n,\eta_n)}$ denotes the distribution function of the random vector (θ_n, η_n).

Proof. Let $\mathcal{F}_n^* = \sigma(Z_0, (\theta_0, \eta_0), \dots, Z_n, (\theta_n, \eta_n))$. Since L_η is a superadditive function, and $s \in [0, 1]$, we deduce, for $n \in \mathbb{Z}^+$, that

$$
\begin{aligned}
g_{n+1}(s) &= \mathrm{E}[\mathrm{E}[s^{Z_{n+1}} \mid \mathcal{F}_n^*]] \\
&= \int_{\mathscr{S}} \sum_{k=0}^{\infty} \mathrm{E}[s^{L_\eta(\sum_{i=1}^k f_{n,i;\theta}, \sum_{i=1}^k m_{n,i;\theta})}] \, \mathrm{P}(Z_n = k) \, \mathrm{d}F_{(\theta_n, \eta_n)}(\theta, \eta) \\
&\leq \int_{\mathscr{S}} \sum_{k=0}^{\infty} \mathrm{E}[s^{\sum_{i=1}^k L_\eta(f_{n,i;\theta}, m_{n,i;\theta})}] \, \mathrm{P}(Z_n = k) \, \mathrm{d}F_{(\theta_n, \eta_n)}(\theta, \eta) \\
&= \int_{\mathscr{S}} \sum_{k=0}^{\infty} (\mathrm{E}[s^{L_\eta(f_{n,1;\theta}, m_{n,1;\theta})}])^k \, \mathrm{P}(Z_n = k) \, \mathrm{d}F_{(\theta_n, \eta_n)}(\theta, \eta) \\
&= \int_{\mathscr{S}} g_n(\zeta_{n;(\theta, \eta)}(s)) \, \mathrm{d}F_{(\theta_n, \eta_n)}(\theta, \eta), \qquad s \in [0, 1].
\end{aligned}
$$

Proposition 3.3. *For $n \in \mathbb{Z}^+$,*

$$
g_{n+1}(s) \geq \int_{\mathscr{S}} g_n(\xi_{n;(\theta, \eta)}(s)) \, \mathrm{d}F_{(\theta_n, \eta_n)}(\theta, \eta), \qquad s \in [0, 1],
$$

where $\xi_{n;(\theta, \eta)}(s) = \lim_{k \to \infty} (\mathrm{E}[s^{L_\eta(\sum_{i=1}^k f_{n,i;\theta}, \sum_{i=1}^k m_{n,i;\theta})}])^{1/k}$.

Proof. First, we shall prove that $\xi_{n;(\theta, \eta)}(s)$ exists. To this end, taking n, s, and (θ, η) fixed, consider the function

$$
\tau(k) = \log(\mathrm{E}[s^{L_\eta(\sum_{i=1}^k f_{n,i;\theta}, \sum_{i=1}^k m_{n,i;\theta})}]), \qquad k = 1, 2, \dots.
$$

From the superadditivity property, and using the fact that $(\sum_{i=k+1}^{k+j} f_{n,i;\theta}, \sum_{i=k+1}^{k+j} m_{n,i;\theta})$ and $(\sum_{i=1}^j f_{n,i;\theta}, \sum_{i=1}^j m_{n,i;\theta})$ are identically distributed random vectors, we have

$$
\begin{aligned}
\tau(k+j) &= \log(\mathrm{E}[s^{L_\eta(\sum_{i=1}^{k+j} f_{n,i;\theta}, \sum_{i=1}^{k+j} m_{n,i;\theta})}]) \\
&\leq \log(\mathrm{E}[s^{L_\eta(\sum_{i=1}^k f_{n,i;\theta}, \sum_{i=1}^k m_{n,i;\theta})}]) + \log(\mathrm{E}[s^{L_\eta(\sum_{i=k+1}^{k+j} f_{n,i;\theta}, \sum_{i=k+1}^{k+j} m_{n,i;\theta})}]) \\
&= \log(\mathrm{E}[s^{L_\eta(\sum_{i=1}^k (f_{n,i;\theta}, m_{n,i;\theta}))}]) + \log(\mathrm{E}[s^{L_\eta(\sum_{i=1}^j (f_{n,i;\theta}, m_{n,i;\theta}))}]) \\
&= \tau(k) + \tau(j), \qquad k, j = 1, 2, \dots.
\end{aligned}
$$

It follows that τ is a subadditive function. Hence (see, e.g. Hille and Philips (1957, p. 244)), $\lim_{k \to \infty} k^{-1} \tau(k)$ exists, and, moreover, $\lim_{k \to \infty} k^{-1} \tau(k) = \inf_{k>0} k^{-1} \tau(k)$. Consequently, $\xi_{n;(\theta, \eta)}(s)$ exists, and

$$
\xi_{n;(\theta, \eta)}(s) = \inf_{k>0} (\mathrm{E}[s^{L_\eta(\sum_{i=1}^k f_{n,i;\theta}, \sum_{i=1}^k m_{n,i;\theta})}])^{1/k}. \tag{3.1}
$$

We now prove Proposition 3.3. From (3.1), we obtain, for $n \in \mathbb{Z}^+$,

$$
\begin{aligned}
g_{n+1}(s) &= \mathrm{E}[\mathrm{E}[s^{Z_{n+1}} \mid \mathcal{F}_n^*]] \\
&= \int_{\mathcal{S}} \sum_{k=0}^{\infty} \mathrm{E}[s^{L_\eta(\sum_{i=1}^k f_{n,i;\theta}, \sum_{i=1}^k m_{n,i;\theta})}] \, \mathrm{P}(Z_n = k) \, \mathrm{d}F_{(\theta_n, \eta_n)}(\theta, \eta) \\
&\geq \int_{\mathcal{S}} \sum_{k=0}^{\infty} (\xi_{n;(\theta,\eta)}(s))^k \, \mathrm{P}(Z_n = k) \, \mathrm{d}F_{(\theta_n, \eta_n)}(\theta, \eta) \\
&= \int_{\mathcal{S}} g_n(\xi_{n;(\theta,\eta)}(s)) \, \mathrm{d}F_{(\theta_n, \eta_n)}(\theta, \eta), \qquad s \in [0, 1].
\end{aligned}
$$

Note that, from Propositions 3.2 and 3.3, and using the fact that $Z_0 = N_0$, we have

$$
N_0 \prod_{k=0}^{n} \mathrm{E}[\zeta'_{k;(\theta_k, \eta_k)}(1)] \leq \mathrm{E}[Z_{n+1}] \leq N_0 \prod_{k=0}^{n} \mathrm{E}[\xi'_{k;(\theta_k, \eta_k)}(1)], \qquad n \in \mathbb{Z}^+.
$$

4. Extinction probability

In this section we consider the extinction probability of the two-sex process presented in (2.1). First, we provide some sufficient conditions (Propositions 4.1 and 4.2) that guarantee the property which is the random environment analogue of the extinction-explosion duality in branching process theory. We then take two different probabilistic approaches to establish some results for the extinction probability. The first approach uses the concept of the asymptotic growth rate (Proposition 4.4), and the second considers the comparison with an asexual branching process in a random environment (Proposition 4.5). For simplicity, we shall use $\Psi = \{(\theta_n, \eta_n)\}_{n \geq 0}$ and $\mathcal{F}_\Psi = \sigma((\theta_0, \eta_0), (\theta_1, \eta_1), \ldots)$ to denote the environmental process and the σ-algebra that it generates, respectively.

For every positive integer N, we shall consider the probability conditional on $\mathcal{F}_\Psi$,

$$
\begin{aligned}
\pi_{N;\Psi} = \mathrm{P}\Big(&\lim_{n \to \infty} Z_n = 0 \mid Z_0 = N, \mathcal{F}_\Psi \Big) \\
&+ \mathrm{P}\Big(\lim_{n \to \infty} Z_n = \infty \mid Z_0 = N, \mathcal{F}_\Psi \Big) \quad \text{almost surely (a.s.).}
\end{aligned}
$$

Next, we shall establish sufficient conditions for

$$
\mathrm{P}(\pi_{N;\psi} = 1) = 1, \qquad N = 1, 2, \ldots. \tag{4.1}
$$

Proposition 4.1. *Assume that, for some $n \in \mathbb{Z}^+$,*

$$
\mathrm{P}(\mathrm{P}(f_{n,1;\theta_n} = 0 \mid \theta_n) > 0) = 1 \quad \text{or} \quad \mathrm{P}(\mathrm{P}(m_{n,1;\theta_n} = 0 \mid \theta_n) > 0) = 1.
$$

Then (4.1) holds.

Proof. Let k be a positive integer. Given that $(\theta_n, \eta_n) = (\theta, \eta)$,

$$
\mathrm{P}\Big(L_\eta\Big(\sum_{i=1}^k f_{n,i;\theta}, \sum_{i=1}^k f_{n,i;\theta} \Big) = 0 \Big) \geq \max\{(\mathrm{P}(f_{n,1;\theta} = 0))^k, (\mathrm{P}(m_{n,1;\theta} = 0))^k\}.
$$

Thus, a.s., we have

$$P(Z_{n+1} = 0 \mid Z_n = k, (\theta_n, \eta_n)) \geq \max\{(P(f_{n,1;\theta_n} = 0 \mid \theta_n))^k, (P(m_{n,1;\theta_n} = 0 \mid \theta_n))^k\}.$$

Hence, since, conditionally on Ψ, 0 is an absorbing state for $\{Z_n\}_{n\geq 0}$,

$$P\left(\bigcup_{m=1}^{\infty} \{Z_{n+m} = k\} \,\Big|\, Z_n = k, \mathcal{F}_\Psi\right) \leq 1 - P(Z_{n+1} = 0 \mid Z_n = k, (\theta_n, \eta_n)) < 1 \quad \text{a.s.},$$

and we deduce that k is a transient state. Consequently, for $N = 1, 2, \ldots,$

$$P\left(P\left(\limsup_{n\to\infty}\{Z_n = k\} \,\Big|\, Z_0 = N, \mathcal{F}_\Psi\right) = 0\right) = 1.$$

And, since

$$\left\{\left\{\lim_{n\to\infty} Z_n = 0\right\} \cup \left\{\lim_{n\to\infty} Z_n = \infty\right\}\right\}^c \subset \bigcup_{k\in\mathbb{N}} \limsup_{n\to\infty}\{0 < Z_n \leq k\},$$

the proof is complete.

Proposition 4.2. *Assume that, for $n \in \mathbb{Z}^+$,*

(i) $P(P(f_{n,1;\theta_n} = 0 \mid \theta_n) = 0) = P(P(m_{n,1;\theta_n} = 0 \mid \theta_n) = 0) = 1,$

(ii) $P(P(L_{\eta_n}(1, 1) = 1 \mid \eta_n) = 1) = 1,$

(iii) $P(P(Z_{n+1} = k \mid Z_n = k, (\theta_n, \eta_n)) < 1) = 1, \ k = 1, 2, \ldots.$

Then (4.1) holds.

Proof. By Proposition 4.1, it is sufficient to prove that each positive integer k is a transient state for $\{Z_n\}_{n\geq 0}$. Indeed, conditional on Ψ, using the superadditivity property and assumptions (i) and (ii), we deduce, for $n \in \mathbb{Z}^+$, that

$$Z_{n+1} = L_{\eta_n}\left(\sum_{i=1}^{Z_n} f_{n,i;\theta_n}, \sum_{i=1}^{Z_n} m_{n,i;\theta_n}\right) \geq \sum_{i=1}^{Z_n} L_{\eta_n}(f_{n,i;\theta_n}, m_{n,i;\theta_n}) \geq Z_n \quad \text{a.s.}$$

Therefore,

$$P\left(\bigcup_{m=1}^{\infty}\{Z_{n+m} = k\} \,\Big|\, Z_n = k, \mathcal{F}_\Psi\right) = P(Z_{n+1} = k \mid Z_n = k, (\theta_n, \eta_n)) \quad \text{a.s.}$$

Now, by assumption (iii),

$$P\left(P\left(\bigcup_{m=1}^{\infty}\{Z_{n+m} = k\} \,\Big|\, Z_n = k, \mathcal{F}_\psi\right) < 1\right) = 1.$$

Therefore, k is a transient state for $\{Z_n\}_{n\geq 0}$.

Definition 4.1. Let

$$q_{N;\Psi} = P\left(\lim_{n\to\infty} Z_n = 0 \;\Big|\; Z_0 = N, \mathcal{F}_\Psi\right)$$

be the a.s. defined extinction probability conditional on Ψ when there are initially a positive number, N, of couples in the population. If, for all N, $P(q_{N;\Psi} = 1) = 1$ then the process will become extinct. If, however, there exists a positive integer N such that $P(q_{N;\Psi} < 1) = 1$ then the process will survive.

We now establish some sufficient conditions for the almost-sure extinction of the process $\{(F_n, M_n)\}_{n\geq 1}$. To this end, we shall make a natural extension to the class of processes considered in (2.1) of the concept of the mean growth rate per couple introduced in Bruss (1984) for Daley's bisexual process.

Definition 4.2. Given that $(\theta_n, \eta_n) = (\theta, \eta)$, we define the mean growth rate per couple as

$$R_{n,k;(\theta,\eta)} = k^{-1} E[Z_{n+1} \mid Z_n = k], \qquad k = 1, 2, \ldots.$$

Intuitively, $R_{n,k;(\theta,\eta)}$ represents the expected growth rate per couple when there are k couples in the nth generation and $(\theta_n, \eta_n) = (\theta, \eta)$. It is clear that

$$R_{n,k;(\theta,\eta)} = k^{-1} E\left[L_\eta\left(\sum_{i=1}^{k} f_{n,i;\theta}, \sum_{i=1}^{k} m_{m,i;\theta}\right)\right].$$

We shall write $R_{n;(\theta,\eta)} = \lim_{k\to\infty} R_{n,k;(\theta,\eta)}$ for the asymptotic growth rate when $(\theta_n, \eta_n) = (\theta, \eta)$.

Proposition 4.3. *Assume that* $(\theta_n, \eta_n) = (\theta, \eta)$. *Then,*

$$R_{n;(\theta,\eta)} = \sup_{k>0} R_{n,k:(\theta,\eta)}.$$

Proof. Taking n and (θ, η) fixed, consider the function $\gamma(k) = k R_{n,k;(\theta,\eta)}$. Then,

$$
\begin{aligned}
\gamma(k+j) &= E\left[L_\eta\left(\sum_{i=1}^{k+j} f_{n,i;\theta}, \sum_{i=1}^{k+j} m_{n,i;\theta}\right)\right] \\
&\geq E\left[L_\eta\left(\sum_{i=1}^{k} f_{n,i;\theta}, \sum_{i=1}^{k} m_{n,i;\theta}\right)\right] + E\left[L_\eta\left(\sum_{i=k+1}^{k+j} f_{n,i;\theta}, \sum_{i=k+1}^{k+j} m_{n,i;\theta}\right)\right] \\
&= E\left[L_\eta\left(\sum_{i=1}^{k} f_{n,i;\theta}, \sum_{i=1}^{k} m_{n,i;\theta}\right)\right] + E\left[L_\eta\left(\sum_{i=1}^{j} f_{n,i;\theta}, \sum_{i=1}^{j} m_{n,i;\theta}\right)\right] \\
&= \gamma(k) + \gamma(j), \qquad k, j = 1, 2, \ldots.
\end{aligned}
$$

Thus, γ is a superadditive function, and, therefore (see Hille and Philips (1957)),

$$r_{n;(\theta,\eta)} = \lim_{k\to\infty} r_{n,k;(\theta,\eta)}$$

exists and

$$r_{n;(\theta,\eta)} = \sup_{k>0} r_{n,k;(\theta,\eta)}.$$

By considering the concept of the asymptotic growth rate, the following result provides sufficient conditions for the almost-sure extinction of the two-sex process.

Proposition 4.4. *Assume that* $P(R_{n;(\theta_n,\eta_n)} < 1) = 1$, $n \in \mathbb{Z}^+$, *and that (4.1) holds. Then,*

$$P(q_{N;\Psi} = 1) = 1, \qquad N = 1, 2 \ldots.$$

Proof. Note that $\{Z_n\}_{n\geq 0}$ is a nonnegative supermartingale with respect to the sequence of σ-algebras $\{\mathscr{F}_n^*\}_{n\geq 0}$,

$$\mathscr{F}_n^* = \sigma(Z_0, (\theta_0, \eta_0), \ldots, Z_n, (\theta_n, \eta_n)).$$

In fact, since $P(R_{n;(\theta_n,\eta_n)} < 1) = 1$, $n \in \mathbb{Z}^+$, we have

$$E[Z_{n+1} \mid \mathscr{F}_n^*] \leq Z_n R_{n;(\theta_n,\eta_n)} \leq Z_n \quad \text{a.s.}$$

Hence,

$$P\Big(P\Big(\lim_{n\to\infty} Z_n = \infty \ \Big| \ Z_0 = N, \mathscr{F}_\psi\Big) = 0\Big) = 1.$$

By (4.1), the proof is complete. $\qquad\square$

In the following result, comparison with an asexual branching process in a random environment is used to provide some sufficient conditions for the survival of the two-sex process. To this end, we shall use the probability generating functions introduced in Section 3,

$$\zeta_{n;(\theta,\eta)}(s) = E[s^{L_\eta(f_{n,1;\theta},m_{n,1;\theta})}], \qquad s \in [0,1], n \in \mathbb{Z}^+.$$

Proposition 4.5. *Assume that*

(i) $\sup_{j\geq 0} E[\zeta''_{j;(\theta_j,\eta_j)}(1)(\zeta'_{j;(\theta_j,\eta_j)}(1))^{-2}] < \infty$,

(ii) $\sum_{j=0}^{\infty}(\prod_{i=0}^{j}(E[\zeta'_{i;(\theta_i,\eta_i)}(1)])^{-1})^{-1} < \infty$.

Then there exists a positive integer N such that $P(q_{N;\Psi} < 1) = 1$.

Proof. We introduce the auxiliary process $\{Z_n^*\}_{n\geq 0}$, where $Z_0^* = Z_0 = N_0$ and, for $n \in \mathbb{Z}^+$,

$$Z_{n+1}^* = \sum_{i=1}^{Z_n^*} L_{\eta_n}(f_{n,i;\theta_n}, m_{n,i;\theta_n}).$$

Note that $\{Z_n^*\}_{n\geq 0}$ is an asexual branching process in a random environment, with $\{(\theta_n, \eta_n)\}_{n\geq 0}$ being its environmental sequence (see, e.g. Agresti (1975)). We shall prove by induction on n that the processes $\{Z_n\}_{n\geq 0}$ and $\{Z_n^*\}_{n\geq 0}$ are such that, for all n, $Z_n \geq Z_n^*$ a.s. Indeed, for $n = 0$, we have $Z_0 = Z_0^* = N_0$. Assume that, for some positive n, $Z_n \geq Z_n^*$ a.s. Then, by the superadditivity and the hypothesis of induction, we have

$$Z_{n+1} = L_{\eta_n}\Big(\sum_{i=1}^{Z_n} f_{n,i;\theta_n}, \sum_{i=1}^{Z_n} m_{n,i;\theta_n}\Big)$$

$$\geq \sum_{i=1}^{Z_n} L_{\eta_n}(f_{n,i;\theta_n}, m_{n,i;\theta_n})$$

$$\geq \sum_{i=1}^{Z_n^*} L_{\eta_n}(f_{n,i;\theta_n}, m_{n,i;\theta_n})$$

$$= Z_{n+1}^* \quad \text{a.s.}$$

Hence, for every positive integer N,

$$P\Big(\lim_{n\to\infty} Z_n = 0 \,\Big|\, Z_0 = N, \mathcal{F}_\psi \Big) \leq P\Big(\lim_{n\to\infty} Z_n^* = 0 \,\Big|\, Z_0^* = N, \mathcal{F}_\Psi \Big) \quad \text{a.s.} \qquad (4.2)$$

Now, from requirements (i) and (ii) of Proposition 4.5, we deduce the survival of the asexual process $\{Z_n^*\}_{n\geq 0}$ (for details, see Agresti (1975)). Consequently, from (4.2), we also derive that the process $\{(F_n, M_n)\}_{n\geq 1}$ will survive.

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