DISPERSION AS A SURVIVAL STRATEGY

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ABSTRACT. We consider stochastic growth models to represent population subject to catastrophes. We analyze the subject from different set ups considering or not spatial restrictions, whether dispersion is a good strategy to increase the population viability. We find out it strongly depends on the effect of a catastrophic event, the spatial constraints of the environment and the probability that each exposed individual survives when a disaster strikes.

1. Introduction

Biological populations are often exposed to catastrophic events that cause mass extinction: Epidemics, natural disasters, etc. When mild versions of these disasters occur, survivors may develop strategies to improve the odds of their species survival. Some populations adopt dispersion as a strategy. Individuals of these populations disperse, trying to make new colonies that may succeed settling down depending on the new environment they encounter. Recently, Schinazi [9] and Machado et al. [7] proposed stochastic models for this kind of population dynamics. For these models they concluded that dispersion is a good survival strategy. Earlier, Lanchier [6] considered the basic contact process on the lattice modified so that large sets of individuals are simultaneously removed, which also models catastrophes. In this work there are qualitative results about the effect of the shape of those sets
on the survival of the process, with interesting non-monotonic results, and dispersion is proved to be a better strategy in some contexts.

Moreover, Brockwell et al. [2] and later Artalejo et al. [1] considered a model for the growth of a population (a single colony) subject to collapse. In their model, two types of effects when a disaster strikes were analyzed separately, binomial effect and geometric effect. After the collapse, the survivors remain together in the same colony (there is no dispersion). They carried out an extensive analysis including first extinction time, number of individuals removed, survival time of a tagged individual, and maximum population size reached between two consecutive extinctions. For a nice literature overview and motivation see Kapodistria et al. [5].

Based on the model proposed by Artalejo et al. [1], and adapting some ideas from Schinazi [9] and Machado et al. [7], we analyze growth models of populations subject to disasters, where after the collapse species adopt dispersion as a survival strategy. We show that dispersion is not always a good strategy to avoid the population extinction. It strongly depends on the effect of a catastrophic event, the spatial constraints of the environment and the probability that each exposed individual survives when a disaster strikes.

This paper is divided into four sections. In Section 2 we define and characterize three models for the growth of populations subject to collapses. In Section 3 we compare the three models introduced in Section 2 and determine under what conditions the dispersion is a good strategy for survival, due to space restrictions and the effects when a disaster strikes. Finally, in Section 4 we prove the results from Sections 2 and 3.

2. Growth models

First we describe a model presented in Artalejo et al. [1]. This is a model for a population which sticks together in one colony, without dispersion. The colony gives birth to a new individual at rate $\lambda > 0$,
while collapses happen at rate $\mu$. If at a collapse time the size of the population is $i$, it is reduced to $j$ with probability $\mu_{ij}$. The parameters $\mu_{ij}$ are determined by how the collapse affects the population size. Next we describe two types of effects.

- **Binomial effect:** Disasters reach the individuals simultaneously and independently of everything else. Each individual survives with probability $p < 1$ (dies with probability $q = 1 - p$), meaning that
  \[
  \mu_{ij}^B = \binom{i}{j} p^j q^{i-j}, \quad 0 \leq j \leq i.
  \]

- **Geometric effect:** Disasters reach the individuals sequentially and the effects of a disaster stop as soon as the first individual survives, if there are any survivor. The probability of next individual to survive given that everyone fails up to that point is $p < 1$, which means that
  \[
  \mu_{ij}^G = \begin{cases} 
  q^i, & j = 0 \\
  pq^{i-j}, & 1 \leq j \leq i.
  \end{cases}
  \]

The binomial effect is appropriate when the catastrophe affects the individuals in an independent and even way. The geometric effect would correspond to cases where the decline in the population is halted as soon as any individual survives the catastrophic event. This may be appropriate for some forms of catastrophic epidemics or when the catastrophe has a sequential propagation effect like in the predator-prey models - the predator kills prey until it becomes satisfied. More examples can be found in Artalejo et al. [1] and in Cairns and Pollett [3].

2.1. **Growth model without dispersion.** In Artalejo et al. [1] the authors consider the binomial and the geometric effect separately as alternatives to the total catastrophe rule which instantaneously removes the whole population whenever a catastrophic event occurs.

Here we consider a mixture of both effects, that is, with probability $r$ the group is stricken sequentially (geometric effect) and with probability $1 - r$ the group is stricken simultaneously (binomial effect). More precisely,

\[
\mu_{ij} := r\mu_{ij}^G + (1 - r)\mu_{ij}^B.
\]
We assume that the collapse rate $\mu$ equals 1. The size of the population (number of individuals in the colony) at time $t$ is a continuous time Markov process $\{X(t) : t \geq 0\}$ whose infinitesimal generator $(q_{ij})_{i,j \geq 0}$ is given by

$$q_{ij} = \begin{cases} 
\lambda, & j = i + 1, \ i \geq 0, \\
\mu_{ij}, & 0 \leq j < i, \\
-(\lambda + \sum_{j=0}^{i-1} \mu_{ij}), & i = j, \\
0 & \text{otherwise.}
\end{cases}$$

We also assume $X(0) = 1$ and denote by $C_1^1(p,r,\lambda)$ the process described by $\{X(t) : t \geq 0\}$. When $r = 0$ and $r = 1$, we obtain the models considered in Artalejo et al. [1].

**Theorem 2.1** (Artalejo et al. [1]). Let $X(t)$ a process $C_1^1(p,r,\lambda)$, with $\lambda > 0$ and $0 < p < 1$. Then, extinction (which means $X(t) = 0$ for some $t > 0$) occurs with probability

$$\rho_1(r) = \begin{cases} 
1, & \text{when } r < 1 \\
\min \left\{ \frac{1-p}{\lambda p}, 1 \right\}, & \text{when } r = 1.
\end{cases}$$

Moreover, if $r < 1$, or $r = 1$ and $\lambda p < 1 - p$, the time it takes until extinction has finite expectation.

**Remark 2.2.** The result of Theorem 2.1 has been shown by Artalejo et al. [1] for the cases $r = 0$ and $r = 1$. They use the word extinction to describe the event that $X(t) = 0$, for some $t > 0$, for a process where state 0 is not an absorbing state. In fact the extinction time here is the first hitting time to the state 0. We keep using the word extinction for this model through the paper.

From their result one can see that survival is only possible when the effect is purely geometric ($r = 1$). The reason for that is quite clear: If $r < 1$ the binomial effect strikes at rate $(1 - r) > 0$ so even if one considers $p = 1$ when the geometric effect strikes, the population will die out as proved in Artalejo et al. [1] for the case $r = 0$.

**2.2. Growth model with dispersion but no spatial restriction.** Consider a population of individuals divided into separate colonies.
Each colony begins with an individual. The number of individuals in each colony increases independently according to a Poisson process of rate $\lambda > 0$. Every time an exponential time of mean 1 occurs, the colony collapses through a binomial or a geometric effect and each of the collapse survivors begins a new colony independently of everything else. We denote this process by $C^2(p, r, \lambda)$ and consider it starting from a single colony with just one individual.

The following theorem establishes necessary and sufficient conditions for survival in $C^2(p, r, \lambda)$.

**Theorem 2.3.** The process $C^2(p, r, \lambda)$ survives with positive probability if and only if

$$p(\lambda + 1)^2r \frac{1}{\lambda p + 1} + p(\lambda + 1)(1 - r) > 1. \quad (2.1)$$

Theorem 2.3 shows that, contrary to what happens in $C^1(p, r, \lambda)$, in $C^2(p, r, \lambda)$ the population is able to survive even when the binomial effect may occur ($r < 1$). See example 2.5. In particular, if $r = 0$ (pure binomial effect) the process survives with positive probability whenever $p(\lambda + 1) > 1$.

The next result shows how to compute the probability of extinction, which means, the probability that eventually the system becomes empty.

**Theorem 2.4.** Let $\rho_2(r)$ be the probability of extinction in $C^2(p, r, \lambda)$. Then $\rho_2(r)$ is the smallest non-negative solution of

$$\phi(s) := \frac{1}{1 + \lambda p} \left[ q + \frac{r(\lambda + 1)ps}{1 + \lambda - \lambda s} + \frac{(1 - r)(\lambda + 1)ps}{1 + \lambda p - \lambda ps} \right] = s. \quad (2.2)$$

**Example 2.5.** For $C^2(2/5, r, 1)$

$$\phi(s) = \frac{3}{7} + \frac{4rs}{14 - 7s} + \frac{20(1 - r)s}{49 - 14s}.$$

The smallest non-negative solution for the equation $\phi(s) = s$, is given by

$$\rho_2(r) = \begin{cases} 
1, & r \leq 7/12 \\
\frac{12r + 49 - \sqrt{144r^2 + 1176r + 49}}{28}, & r > 7/12. 
\end{cases}$$
Remark 2.6. For $r = 0$ (pure binomial effect) and $r = 1$ (pure geometric effect) the smallest non-negative solution for (2.2) is:

$$\rho_2(0) = \min \left\{ \frac{q}{\lambda p}, 1 \right\} \quad \text{and} \quad \rho_2(1) = \min \left\{ \frac{q(\lambda + 1)}{\lambda(1 + \lambda p)}, 1 \right\}.$$  

Observe that $\rho_2(0) \geq \rho_2(1)$ where the strict inequality holds provided $(1 + \lambda + \lambda^2)^{-1} < p < 1$. Moreover,

- If $p < \frac{1}{1 + \lambda + \lambda^2}$ then $\rho_2(0) = \rho_2(1) = 1$.
- If $\frac{1}{1 + \lambda + \lambda^2} < p < \frac{1}{1 + \lambda}$ then $\rho_2(0) = 1$ and $\rho_2(1) = \frac{q(\lambda + 1)}{\lambda(1 + \lambda p)}$.
- If $p > \frac{1}{1 + \lambda}$ then $\rho_2(0) = \frac{q}{\lambda p}$ and $\rho_2(1) = \frac{q(\lambda + 1)}{\lambda(1 + \lambda p)}$.

Note that likewise as occurs in $C_1^i(p,r,\lambda)$, the binomial effect is a worst scenario than the geometric effect for the population survival in $C^2(p,r,\lambda)$.

Remark 2.7. Observe that $\rho_1(r) \geq \rho_2(r)$ for $r \in [0,1]$. In addition, if $r < 1$ the inequality is strict provided (2.1) holds. Moreover, $\rho_1(1) > \rho_2(1)$ for $\lambda(1 + \lambda p) > q(\lambda + 1)$. That means when there are no spatial restrictions, dispersion is a good strategy for population survival. That coincides with the results for the models presented and analyzed by Schinazi [9] and Machado et al. [7].

2.3. Growth with dispersion and spatial restriction. Let $G_m$ be a graph (finite or infinite) such that every vertex has $m$ neighbours, what is known as a $m-$regular graph. Let us define a process with dispersion and spatial restrictions on $G_m$, starting from a single colony placed at one vertex of $G_m$, with just one individual. The number of individuals in a colony grows following a Poisson process of rate $\lambda > 0$. To each colony we associate an exponential time of mean 1 that indicates when the colony collapses. Each one of the individuals that survived the collapse (either a binomial or a geometric effect) picks randomly a neighbor vertex and tries to create a new colony at it. Among the survivors leaping to the same vertex trying to create a new colony at it, only one succeeds (disregarding the number of colonies
already present at that vertex), the others die. So in this case when a colony collapses, it is replaced by 0, 1, ... or \( m \) colonies. Finally, every vertex can have any number of independent colonies. We denote this process by \( C^3(p, r, \lambda, m) \).

The next result presents a necessary and sufficient condition for population survival in \( C^3(p, r, \lambda, m) \).

**Theorem 2.8.** The process \( C^3(p, r, \lambda, m) \) survives with positive probability if and only if

\[
\frac{mp(1 + \lambda)^2 r}{(m + \lambda)(\lambda p + 1)} + \frac{mp(1 + \lambda)(1 - r)}{m + \lambda p} > 1.
\]

The following result shows that the extinction probability for the process \( C^3(p, r, \lambda, m) \) can be computed as the root of a polynomial of degree \( m \).

**Theorem 2.9.** Let \( \rho_3(r) \) be the probability of population extinction in \( C^3(p, r, \lambda, m) \). Then \( \rho_3(r) \) is the smallest non-negative solution of

\[
\psi(s) := r\psi_G(s) + (1 - r)\psi_B(s) = s,
\]

where

\[
\psi_B(s) := \frac{q}{1 + \lambda p} + \frac{m(1 + \lambda)}{\lambda p + 1} \sum_{k=1}^{m} \binom{m}{k} \left[ \frac{-\lambda ps}{m(1 + \lambda p)} \right]^k \sum_{j=0}^{k-1} \binom{k}{j} \frac{(-1)^{j}j^{k}}{m(1 + \lambda p) - \lambda p j},
\]

\[
\psi_G(s) := \frac{q}{1 + \lambda p} + \frac{(1 + \lambda)ps}{\lambda p + 1} \sum_{k=1}^{m} \binom{m}{k} \left[ \frac{-\lambda s}{m(1 + \lambda)} \right]^{k-1} \sum_{j=0}^{k-1} \binom{k}{j} \frac{(-1)^{j-1}j^{k}}{m(1 + \lambda) - \lambda j}.
\]

**Example 2.10.** Consider \( C^3(2/3, r, 1, 3) \). Then

\[
\psi(s) = \left( \frac{126r}{3575} + \frac{32}{715} \right) s^3 + \left( \frac{138r}{3575} + \frac{144}{715} \right) s^2 + \left( \frac{36}{65} - \frac{24r}{325} \right) s + \frac{1}{5}.
\]

Therefore, the smallest non-negative solution for \( \psi(s) = s \) is given by

\[
\rho_3(r) = \frac{-440 - 132r + \sqrt{22(14000 + 9375r + 792r^2)}}{2(80 + 63r)}.
\]
3. Dispersion as a survival strategy

Towards being able to evaluate dispersion as a survival strategy we define

\[ \lambda^i(p, r) := \inf \{ \lambda : \mathbb{P}[C^i(p, r, \lambda) \text{ survives}] > 0 \}, \quad \text{for } i = 1, 2 \]

and \[ \lambda^3(p, r, m) := \inf \{ \lambda : \mathbb{P}[C^3(p, r, \lambda, m) \text{ survives}] > 0 \}. \]

Observe that for \( i = 1, 2 \), when \( 0 < \lambda^i(p, r) < \infty \) for \( 0 < p < 1 \), the graph of \( \lambda^i(p, r) \) splits the parametric space \( \lambda \times p \) into two regions. For those values of \( (\lambda, p) \) above the curve \( \lambda^i(p, r) \) there is survival in \( C^i(p, r, \lambda) \) with positive probability, and for those values of \( (\lambda, p) \) below the curve \( \lambda^i(p, r) \) extinction occurs in \( C^i(p, r, \lambda) \) with probability 1. The analogous happens also for \( i = 3 \) and any \( m \).

Next we establish some properties of \( \lambda^2(p, r) \) and \( \lambda^3(p, r, m) \).

**Proposition 3.1.** Let \( 0 \leq r \leq 1 \) and \( 0 < p < 1 \). Then,

(i) \( 0 < \lambda^2(p, r) < \lambda^3(p, r, m + 1) < \lambda^3(p, r, m) < \infty \), for all \( m \geq 2 \).

Besides \( \lambda^3(p, r, 1) = \infty \).

(ii) \( \lim_{m \to \infty} \lambda^3(p, r, m) = \lambda^2(p, r) \).

**Remark 3.2.** From standard coupling arguments one can show the expected monotonicity relationship.

If \( p_1 > p_2 \) then

\[ \lambda^i(p_1, r) \leq \lambda^i(p_2, r), \quad i = 1, 2 \]

\[ \lambda^3(p_1, r, m) \leq \lambda^3(p_2, r, m). \]

If \( r_1 > r_2 \) then

\[ \lambda^i(p, r_1) \leq \lambda^i(p, r_2), \quad i = 1, 2 \]

\[ \lambda^3(p, r_1, m) \leq \lambda^3(p, r_2, m). \]

For what follows \( 0 < p < 1 \). From Theorem 2.1 it follows that if \( r < 1 \) then \( \lambda^1(p, r) = \infty \), and from Proposition 3.1 we obtain that

\[ \lambda^2(p, r) < \lambda^3(p, r, m) < \lambda^1(p, r), \]
for all $m \geq 2$. Then, provided binomial effect may strike ($r < 1$), dispersion is a good scenario for population survival either with or without spatial restrictions.

When binomial effect is not present ($r = 1$), which means, only geometric effect is present, it is simple to compute $\lambda^1(p, 1)$, $\lambda^2(p, 1)$ and $\lambda^3(p, 1, m)$. From Theorems 2.1, 2.3 and 2.8 we have that

$$\lambda^1(p, 1) = \frac{1-p}{p},$$
$$\lambda^2(p, 1) = \sqrt{1 + \frac{1-p}{p} - \frac{1}{2}},$$
$$\lambda^3(p, 1, m) = \frac{1 - mp + \sqrt{(1 - mp)^2 + 4m(m-1)p(1-p)}}{2p(m-1)}.$$

When $r = 1$ (pure geometric effect) $\lambda^2(p, 1) < \lambda^1(p, 1)$. However, dispersion is not always a better scenario for population survival, as one can see in Figure 1. Observe that

$$\lambda^3(p, 1, m) \leq \lambda^1(p, 1) \iff p \leq 1 - \frac{1}{m-1}.$$ 

Therefore, under a pure geometric effect, dispersion is an advantage or not for population survival depending on both $m$, the spatial restrictions, and $p$, the probability that an individual, when exposed to catastrophe, survives. See Figure 2.

4. Proofs

Theorem 2.1 is part of Theorem 3.1 and Theorem 3.2 in Artalejo et al. They work hard with the moment generating functions of the first excursion until 0 (the empty state) when the process (binomial and geometric catastrophes) starts from 1 individual. Here we present an alternative proof for $r < 1$ by the use of Foster’s theorem, enunciated next. For a proof of Foster’s theorem see Fayolle et al. Theorem 2.2.3].
Figure 1. Graphics of $\lambda^1(p, 1), \lambda^2(p, 1), \lambda^3(p, 1, 5)$

Figure 2. Curve $p = 1 - (m - 1)^{-1}$. Best strategy for survival, when $r=1$, provided the spatial restrictions ($m$) and the probability that an individual survives when facing a collapse ($p$).
**Theorem 4.1** (Foster’s theorem). Let \( \{W_n\}_{n \geq 0} \) be an irreducible and aperiodic Markov chain on countable state space \( \mathcal{A} = \{\alpha_i, \ i \geq 0\} \). Then, \( \{W_n\}_{n \geq 0} \) is ergodic if and only if there exists a positive function \( f(\alpha) \), \( \alpha \in \mathcal{A} \), a number \( \epsilon > 0 \) and a finite set \( A \subset \mathcal{A} \) such that

\[
\mathbb{E}[f(W_{n+1}) - f(W_n) \mid W_n = \alpha_j] \leq -\epsilon, \quad \alpha_j \notin A,
\]

\[
\mathbb{E}[f(W_{n+1}) \mid W_n = \alpha_i] < \infty, \quad \alpha_i \in A.
\]

Next we present the proof of Theorem 2.1.

**Proof of Theorem 2.1.** Let \( \{Y_n\}_{n \geq 0} \) be a discrete-time Markov chain embedded on \( C^1(p, r, \lambda) \), with transition probabilities given by

\[
P_{i,i+1} = \frac{\lambda}{\lambda + 1}, \quad i \geq 0,
\]

\[
P_{i,j} = \frac{r\mu^G_{ij} + (1-r)\mu^B_{ij}}{\lambda + 1}, \quad 0 \leq j \leq i.
\]

Ergodicity of \( \{Y_n\} \) implies that the time until extinction of \( C^1(p, r, \lambda) \) has finite mean.

Observe that \( \{Y_n\} \) is irreducible and aperiodic. We use Foster’s theorem to show that \( \{Y_n\}_{n \geq 0} \) is ergodic for \( 0 \leq r < 1, \ 0 < p < 1 \) and \( \lambda > 0 \). Consider the function \( f : \mathbb{N} \to \mathbb{R}^+ \) defined by \( f(i) = i + 1, \ \epsilon > 0 \) and the set

\[
A := \left\{ i \in \mathbb{N} : \frac{\lambda - i(1-r)q}{1+\lambda} - \frac{rq(1-q^i)}{p(1+\lambda)} > -\epsilon \right\}.
\]

For \( 0 \leq r < 1, \ 0 < p < 1 \) and \( \lambda > 0 \), the set \( A \) is finite. Moreover we have that
\[
\mathbb{E}[f(Y_{n+1}) | Y_n = i] = \sum_{j=0}^{i+1} [f(j) - f(i)]P_{i,j}
\]

\[
= \frac{\lambda}{1+\lambda} + \sum_{j=0}^{i} (j-i) \left( \frac{r\mu_{ij}^G + (1-r)\mu_{ij}^B}{1+\lambda} \right)
\]

\[
= \frac{\lambda}{1+\lambda} + \frac{1}{1+\lambda} \left[ -riq^j + r \sum_{j=1}^{i} (j-i)pq^{i-j} \right]
\]

\[
+ (1-r) \sum_{j=0}^{i} (j-i) \binom{i}{j} p^j q^{i-j}
\]

\[
= \frac{\lambda - i(1-r)q}{1+\lambda} - \frac{rq(1-q^i)}{p(1+\lambda)}
\]

\[
\leq -\epsilon \quad \text{for} \quad i \notin A.
\]

\[
\mathbb{E}[f(Y_{n+1}) | Y_n = i] = \sum_{j=0}^{i+1} f(j)P_{i,j} \leq (i + 2)^2 < \infty \quad \text{for} \quad i \in A.
\]

It follows from Foster’s theorem that \( \{Y_n\} \) is ergodic and that concludes the proof. \( \square \)

Seeking the proof of the other results we define the following auxiliary process.

**Auxiliary process** \( (Z_{n}^{r,i})_{n \geq 0} \):

Consider \( C^2(p, r, \lambda) \) and \( C^3(p, r, \lambda, m) \). We define \( Z_{n}^{r,i} = 1 \) for \( i = 2, 3 \), the number of colonies present at time 0 in each model. As soon as it collapses, \( Z_{1}^{r,i} \), a random number of colonies will be created, the first generation. Each one of these colonies will give birth (at different times) to a random number of new colonies, the second generation. Let us define this quantity by \( Z_{2}^{r,i} \). In general, for \( n \geq 1 \), if \( Z_{n-1}^{r,i} = 0 \) then \( Z_{n}^{r,i} = 0 \). On the other hand, if \( Z_{n-1}^{r,i} \geq 1 \) then \( Z_{n}^{r,i} \) is the number of colonies generated by the \((n - 1)\)th generation of colonies.
From the fact that the numbers of descendants of different colonies are independent and have the same distribution, we claim that \( \{ Z_n^{r,i} \}_{n \in \mathbb{N}} \) is a Galton-Watson process.

**Remark 4.2.** For \( i = 2, 3 \), observe that \( C^i(p, r, \lambda) \) dies out if and only if \( \{ Z_n^{r,i} \}_{n \in \mathbb{N}} \) dies out, which in turn happens almost surely if and only if \( \mathbb{E}[Z_1^{r,i}] \leq 1 \). The probability of extinction for \( \{ Z_n^{r,i} \}_{n \in \mathbb{N}} \) is the smallest non-negative solution of \( \phi_{r,i}(s) = s \), where \( \phi_{r,i}(s) \) is the probability generating function of \( Z_1^{r,i} \).

**Lemma 4.3.** The probability generating function of \( Z_1^{r,2} \) is given by:

\[
\phi_{r,2}(s) = \frac{1}{1 + \lambda p} \left[ q + \frac{r(\lambda + 1)ps}{1 + \lambda - \lambda s} + \frac{(1 - r)(\lambda + 1)ps}{1 + \lambda p - \lambda ps} \right]
\]

and

\[
\mathbb{E}[Z_1^{r,2}] = \frac{p(\lambda + 1)^2r}{\lambda p + 1} + p(\lambda + 1)(1 - r).
\]

**Proof.** \( Z_1^{r,2} \) is the number of colonies in the first generation of \( C^2(p, r, \lambda) \).

Denote \( Z_B := Z_1^{0,2} \) and \( Z_G := Z_1^{1,2} \). Firstly we show that

\[
\mathbb{P}[Z_B = k] = \begin{cases} \frac{1 + \lambda}{\lambda (1 + \lambda p)} \left( \frac{\lambda p}{1 + \lambda p} \right)^k, & k \geq 1 \\ q \frac{1}{1 + \lambda p}, & k = 0 \end{cases} \quad (4.1)
\]

\[
\mathbb{P}[Z_G = k] = \begin{cases} \frac{p}{1 + \lambda p} \left( \frac{\lambda}{1 + \lambda} \right)^{k-1}, & k \geq 1 \\ q \frac{1}{1 + \lambda p}, & k = 0 \end{cases} \quad (4.2)
\]

**Definition 4.4.** Let us consider the following random variables

- \( T \) the lifetime of the colony until the collapse time;
- \( f_T(t) \) the density of the random variable \( T \);
- \( X_T \) the amount of individuals created in a colony until it collapses.
Observe that

\[ P[Z_B = k] = \int_0^\infty f_T(t) \sum_{n=0}^{\infty} P(X_T = n|T = t)P(Z_B = k|X_T = n; T = t)dt. \quad (4.3) \]

Then, for \( k = 0 \), we have that

\[ P[Z_B = 0] = \int_0^\infty e^{-t} \sum_{n=0}^{\infty} \frac{e^{-\lambda t} (\lambda t)^n}{n!} q^{n+1} dt = q \int_0^\infty e^{-(\lambda p+1)t} dt = \frac{q}{1 + \lambda p}. \]

For \( k \geq 1 \),

\[
P[Z_B = k] = \int_0^\infty e^{-t} \sum_{n=k-1}^{\infty} \frac{e^{-\lambda t} (\lambda t)^n}{n!} \binom{n+1}{k} p^k q^{n+1-k} dt \\
= q \left( \frac{p}{q} \right)^k \sum_{n=k-1}^{\infty} \binom{n+1}{k} \frac{(\lambda q)^n}{n!} \int_0^\infty e^{-(\lambda p+1)t} t^n dt \\
= q \left( \frac{p}{q} \right)^k \sum_{n=k-1}^{\infty} \binom{n+1}{k} \frac{(\lambda q)^n}{n!} \frac{\Gamma(n+1)}{(\lambda + 1)^{n+1}} \\
= q \frac{1}{\lambda + 1} \left( \frac{p}{q} \right)^k \sum_{n=k-1}^{\infty} \binom{n+1}{k} \left( \frac{\lambda q}{\lambda + 1} \right)^n \\
= q \frac{1}{\lambda + 1} \left( \frac{p}{q} \right)^k \left( \frac{\lambda q}{\lambda + 1} \right)^{k-1} \sum_{j=0}^{\infty} \binom{j+k}{k} \left( \frac{\lambda q}{\lambda + 1} \right)^j \\
= q \frac{1}{\lambda + 1} \left( \frac{p}{q} \right)^k \left( \frac{\lambda q}{\lambda + 1} \right)^{k-1} \left( 1 - \frac{\lambda q}{\lambda + 1} \right)^{-(k+1)} \\
= \frac{1 + \lambda}{\lambda(1 + \lambda p)} \left( \frac{\lambda p}{1 + \lambda p} \right)^k.
\]
Similarly to (4.3), we obtain the distribution of $Z_G$. First observe that $P[Z_B = 0] = P[Z_G = 0]$. Besides, for $k \geq 1$,

$$P[Z_G = k] = \int_0^\infty e^{-t} \sum_{n=k-1}^{\infty} \frac{e^{-\lambda t}(\lambda t)^n}{n!} p q^{n+1-k} dt$$

$$= pq^{1-k} \sum_{n=k-1}^{\infty} \frac{(q \lambda)^n}{n!} \int_0^\infty e^{-(\lambda+1)t} t^n dt$$

$$= pq^{1-k} \sum_{n=k-1}^{\infty} \frac{(q \lambda)^n}{n!} \frac{\Gamma(n+1)}{(\lambda+1)^{n+1}}$$

$$= \frac{pq^{1-k}}{\lambda+1} \sum_{n=k-1}^{\infty} \left( \frac{q \lambda}{\lambda+1} \right)^n$$

$$= \frac{pq^{1-k}}{\lambda+1} \left( \frac{q \lambda}{\lambda+1} \right)^{k-1} \sum_{j=0}^{\infty} \left( \frac{q \lambda}{\lambda+1} \right)^j$$

$$= \frac{p}{1 + \lambda p} \left( \frac{\lambda}{\lambda+1} \right)^{k-1}.$$ 

By (4.1) we obtain the probability generating function of $Z_B$,

$$\phi_B(s) = E[s^{Z_B}] = \sum_{k \geq 0} P[Z_B = k] s^k$$

$$= \frac{q}{1 + \lambda p} + \frac{1 + \lambda}{\lambda(1 + \lambda p)} \sum_{k \geq 1} \left( \frac{\lambda p s}{1 + \lambda} \right)^k$$

$$= \frac{1}{1 + \lambda p} \left[ q + \frac{(\lambda + 1)ps}{1 + \lambda p - \lambda ps} \right].$$

Besides, from (4.2), we obtain the probability generating function of $Z_G$,

$$\phi_G(s) = E[s^{Z_G}] = \sum_{k \geq 0} P[Z_G = k] s^k$$

$$= \frac{q}{1 + \lambda p} + \frac{sp}{1 + \lambda p} \sum_{k \geq 1} \left( \frac{\lambda s}{1 + \lambda} \right)^{k-1}$$

$$= \frac{1}{1 + \lambda p} \left[ q + \frac{(\lambda + 1)ps}{1 + \lambda - \lambda s} \right].$$

Finally, the desired result follows after we observe that

$$\phi_{r,2}(s) = r \phi_G(s) + (1 - r) \phi_B(s),$$
and computing $\mathbb{E}[Z_{r,2}^2] = \phi_{r,2}'(1)$.

\[\begin{align*}
\text{Lemma 4.5.} & \quad \text{The probability generating function of } Z_{r,3}^1 \text{ is given by:} \\
& \psi_{r,3}(s) = r\psi_G(s) + (1 - r)\psi_B(s), \\
& \text{where} \\
& \psi_B(s) := \frac{q}{1 + \lambda p} + \frac{m(1 + \lambda)}{\lambda} \sum_{k=1}^{m} \binom{m}{k} \left[ -\frac{\lambda ps}{m(1 + \lambda p)} \right]^k \sum_{j=0}^{k} \binom{k}{j} \frac{(-1)^j k^j}{m(1 + \lambda p) - \lambda pj}, \\
& \psi_G(s) := \frac{q}{1 + \lambda p} + \frac{(1 + \lambda)ps}{\lambda p + 1} \sum_{k=1}^{m} \binom{m}{k} \left[ -\frac{\lambda s}{m(1 + \lambda)} \right]^{k-1} \sum_{j=0}^{k} \binom{k}{j} \frac{(-1)^{j-1} k^j}{m(1 + \lambda) - \lambda j}.
\end{align*}\]

Furthermore,

\[\mathbb{E}[Z_{r,3}^1] = \frac{mp(\lambda + 1)^2 r}{(m + \lambda)(\lambda p + 1)} + \frac{mp(\lambda + 1)(1 - r)}{m + \lambda p}.\]

\textbf{Proof.} Consider $C_3(p, r, \lambda, m)$ starting from one colony placed at some vertex $x \in G_m$. Besides the quantity already defined $Z_{r,3}^1$, consider also $Z$ the number of individuals that survived right after the collapse, before they compete for space.

From the definition of $C_3(p, r, \lambda, m)$ it follows that

\[\mathbb{P}[Z = j] = r\mathbb{P}[Z_G = j] + (1 - r)\mathbb{P}[Z_B = j],\]

where $Z_B$ and $Z_G$ are the random variables defined in (4.1) and (4.2), respectively. By other side, for $k \in \{1, \ldots, m\}$ and $j \geq k$, observe that

\[\mathbb{P}[Z_{r,3}^1 = k | Z = j] = \binom{m}{k} \frac{T(j, k)}{m^j}.\]

By the inclusion-exclusion principle, $T(j, k) = \sum_{i=0}^{k} \binom{k}{i} (-1)^i (k - i)^j$ is the number of surjective functions whose domain is a set with $j$ elements and whose codomain is a set with $k$ elements. See Tucker [10] p. 319.
Then, for \( k \in \{1, \ldots, m\} \),

\[
\mathbb{P}[Z_{r_3}^r = k] = r \sum_{j=k}^{\infty} \binom{m}{k} \frac{T(j, k)}{m^j} \mathbb{P}[Z_G = j] + (1 - r) \sum_{j=k}^{\infty} \binom{m}{k} \frac{T(j, k)}{m^j} \mathbb{P}[Z_B = j]. \tag{4.5}
\]

By (4.1), we have that

\[
\sum_{j=k}^{\infty} \binom{m}{k} \frac{T(j, k)}{m^j} \mathbb{P}[Z_B = j] = \binom{m}{k} \left(1 + \frac{\lambda}{\lambda p + 1} \sum_{i=0}^{k} \binom{k}{i} \frac{(-1)^i(k-i)^i}{m(\lambda p + 1)} \right).
\]

Similarly, by (4.2), we have that

\[
\sum_{j=k}^{\infty} \binom{m}{k} \frac{T(j, k)}{m^j} \mathbb{P}[Z_B = j] = \binom{m}{k} \left(1 + \frac{\lambda}{\lambda p + 1} \sum_{i=0}^{k} \binom{k}{i} \frac{(-1)^i(k-i)^i}{m(\lambda p + 1)} \right).
\]

Similarly, by (4.2), we have that
\[
\sum_{j=k}^{\infty} \binom{m}{j} \frac{T(j,k)}{m^j} P[Z_G = j]
\]
\[
= \binom{m}{k} \frac{p}{m(\lambda p + 1)} \sum_{j=k}^{\infty} \left[ \frac{\lambda}{m(\lambda + 1)} \right]^{j-1} T(j,k)
\]
\[
= \binom{m}{k} \frac{p}{m(\lambda p + 1)} \left[ \frac{\lambda}{m(\lambda + 1)} \right]^{k-1} \sum_{j=0}^{\infty} \left[ \frac{\lambda}{m(\lambda + 1)} \right]^{j} T(j+k,k)
\]
\[
= \binom{m}{k} \frac{p}{m(\lambda p + 1)} \left[ \frac{\lambda}{m(\lambda + 1)} \right]^{k-1} \sum_{j=0}^{\infty} \sum_{i=0}^{k} \binom{k}{i} (-1)^i (k-i)^{j+k}
\]
\[
= \binom{m}{k} \frac{p}{m(\lambda p + 1)} \left[ \frac{\lambda}{m(\lambda + 1)} \right]^{k-1} \sum_{i=0}^{k} \binom{k}{i} \left( \frac{\lambda(k-i)}{m(\lambda + 1)} \right)^j
\]
\[
= \binom{m}{k} (1 + \lambda) p \left[ \frac{\lambda}{m(1+\lambda)} \right]^{k-1} \sum_{i=0}^{k} \binom{k}{i} \frac{(-1)^i (k-i)^{k}}{m(1+\lambda) - \lambda(k-i)}.
\] (4.7)

Finally, observe that \( P[Z_{1,3}^r = 0] = P[Z = 0] = q/(1 + \lambda p) \). With (4.4), (4.6) and (4.7) we obtain the probability generating function of \( Z_{1,3}^r \).

To compute \( E[Z_{1,3}^r] \), consider enumerating each neighbour of the initial vertex \( x \), from 1 to \( m \). Next we describe \( Z_{1,3}^r = \sum_{i=1}^{m} I_i \), where \( I_i \) is the indicator function of the event \( \{ \text{A new colony is created in the first generation at the } i^{th} \text{ neighbour vertex of } x \} \). Therefore,
\[
E[Z_{1,3}^r] = \sum_{i=1}^{m} P[I_i = 1] = mP[I_1 = 1].
\] (4.8)

Observe that
\[
P[I_1 = 1|Z = k] = 1 - \left( \frac{m-1}{m} \right)^k
\]
and that by using (4.4) we have that
\[
P[I_1 = 1] = r \sum_{k=1}^{\infty} \left[ 1 - \left( \frac{m-1}{m} \right)^k \right] P[Z_G = k]
\]
\[
+ (1 - r) \sum_{k=1}^{\infty} \left[ 1 - \left( \frac{m-1}{m} \right)^k \right] P[Z_B = k].
\] (4.9)
Substituting (4.1) and (4.2) in (4.9) one can see that
\[
P[I_1 = 1] = \frac{p(\lambda + 1)^2r}{(m + \lambda)(\lambda p + 1)} + \frac{p(\lambda + 1)(1 - r)}{m + \lambda p}.
\] (4.10)

Finally, plugging (4.10) into (4.8) we obtain the desired result. □

Proofs of Theorems 2.3 and 2.8. From Remark 4.2 one can see that
\(C^i(p, r, \lambda)\) survives if and only if
\(\mathbb{E}[Z^{r, i}] > 1\). From Lemmas 4.3 and 4.5 the result follows. □

Proofs of Theorems 2.4 and 2.9. From Remark 4.2 we have that the probabilities of extinction, \(\rho_2(r)\) and \(\rho_3(r)\), of \(C^2(p, r, \lambda)\) and \(C^3(p, r, \lambda, m)\), are the smallest solution in \([0, 1]\) of \(\varphi_{r, i}(s) = s\) for \(i = 2\) and \(3\) respectively. The desired results follow from Lemmas 4.3 and 4.5. □

Proof of Proposition 3.1 (i). First we define the following functions
\[
f_m(\lambda) := \frac{mp(1 + \lambda)^2r}{(m + \lambda)(\lambda p + 1)} + \frac{mp(1 + \lambda)(1 - r)}{m + \lambda p},
\]
\[
f(\lambda) := \frac{p(\lambda + 1)^2r}{\lambda p + 1} + p(\lambda + 1)(1 - r).
\]
From Theorems 2.3 and 2.8 it follows that
\[
\lambda^2(p, r) = \inf \{\lambda : f(\lambda) > 1\},
\]
\[
\lambda^3(p, r, m) = \inf \{\lambda : f_m(\lambda) > 1\}.
\]

Observe that \(f_m\) and \(f\) are continuous functions on \([0, \infty)\), such that \(f_m(0) = f(0) = p < 1\), \(\lim_{\lambda \to \infty} f(\lambda) = \infty\) and \(\lim_{\lambda \to \infty} f_m(\lambda) = m\).

Moreover, \(\{f_m\}_{m \geq 1}\) is a strictly increasing sequence of strictly increasing functions on \((0, \infty)\) such that \(\lim_{m \to \infty} f_m(\lambda) = f(\lambda)\). Similarly, \(f\) is a strictly increasing function.

Then, from the intermediate value theorem and the strict monotonicity of \(f\) we have that there is a unique \(\lambda_* \in (0, \infty)\) such that \(f(\lambda_*) = 1\). Moreover, from the definition of \(\lambda^2(p, r)\) and the continuity of \(f\), we have that
\[
f(\lambda) = 1 \iff \lambda = \lambda^2(p, r).
\] (4.11)
Thus, $\lambda_* = \lambda^2(p,r)$. Similarly, for $m \geq 2$, we obtain that
$$\lambda^3(p,r,m) \in (0, \infty)$$
and
$$f_m(\lambda) = 1 \iff \lambda = \lambda^3(p,r,m).$$
Besides, from the strict monotonicity of $f_1$, it follows that
$$\lambda^3(p,r,1) = \infty.$$

In order to show that $\lambda^3(p,r,m) > \lambda^3(p,r,m + 1)$ for all $m \geq 2$ let us assume that $\lambda^3(p,r,m) \leq \lambda^3(p,r,m + 1)$ for some $m \geq 2$ and proceed by contradiction. Note that
$$1 = f_m(\lambda^3(p,r,m)) \leq f_m(\lambda^3(p,r,m + 1)) < f_{m+1}(\lambda^3(p,r,m + 1)) = 1$$
which is clearly a contradiction. Analogously one can show that
$$\lambda^2(p,r) < \lambda^3(p,r,m)$$
for all $m \geq 1$.

\[\square\]

5. Acknowledgments

The authors are thankful to Rinaldo Schinazi and Elcio Lebensztayn for helpful discussions about the model. V. Junior and A. Roldán wish to thank the Instituto de Matemática e Estatística of Universidade de São Paulo for the warm hospitality during their scientific visits to that
institute. The authors are thankful for the two anonymous referees for a careful reading and many suggestions and corrections that greatly helped to improve the paper.

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