



Deposited via The University of Leeds.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/id/eprint/90147/>

Version: Accepted Version

Article:

Gomez-Corral, A and Lopez Garcia, M (2015) Lifetime and reproduction of a marked individual in a two-species competition process. *Applied Mathematics and Computation*, 264. 223 - 245. ISSN: 0096-3003

<https://doi.org/10.1016/j.amc.2015.04.061>

(c) 2015, Elsevier. Licensed under the Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International <http://creativecommons.org/licenses/by-nc-nd/4.0/>

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

Lifetime and reproduction of a marked individual in a two-species competition process

A. Gómez-Corral^{a,b,*}, M. López-García^c

^a*ICMAT – Institute of Mathematical Sciences, Calle Nicolás Cabrera 13-15, Campus de Cantoblanco UAM, 28049-Madrid, Spain*

^b*Department of Statistics and OR, Faculty of Mathematics, Plaza de Ciencias 3, 28040-Madrid, Spain*

^c*Department of Applied Mathematics, School of Mathematics, University of Leeds, Leeds LS2 9JT, United Kingdom*

Abstract

The interest is in a stochastic model for the competition of two species, which was first introduced by Reuter [16] and Iglehart [10], and then analyzed by Ridler-Rowe [17]. The model is related to the two-species autonomous competitive model (Zeeman [21]), where individuals compete either directly or indirectly for a limited food supply and, consequently, births and death rates depend on the population sizes of one or both of the species. The aim is to complement the treatment of the model we started in [7, 8] by focusing here on probabilistic descriptors that are inherently linked to an individual: its residual lifetime and the number of direct descendants. We present an approximating model based on the maximum size distribution, and we discuss on various models defined in terms of the underlying killing and reproductive strategies. Numerical examples are presented to show the effects of the killing and reproductive strategies on the behavior of an individual, and how the impact of these strategies on the descriptors vanishes in highly competitive ecosystems.

Keywords: Bivariate birth-and-death process; competition process; lifetime; Markov chain model; number of descendants; survival

2000 MSC: 92D25

1. Introduction

The two-species competition process is a simple mathematical model which has been studied extensively from deterministic (Allen [2]) and stochastic (Allen

*Corresponding author

Email addresses: antonio.gomez@icmat.es (A. Gómez-Corral),
m.lopezgarcia@leeds.ac.uk (M. López-García)

URL: <http://www.icmat.es/antonio.gomez-corral> (A. Gómez-Corral),
<https://www1.maths.leeds.ac.uk/~lopezgarcia/index.html> (M. López-García)

[1]) perspectives under a variety of assumptions. A competitive interaction between two species is one of the basic interspecies relations for biological, ecological and social networks, and it is characterized by the fact that individuals compete either directly or indirectly for common resources in such a way that an increase in the density of one species results in a decrease in the other species that is proportional to the product of both species. The classical work, assuming stochastic models, dates as far back as Iglehart [10] and Reuter [16]; more concretely, Reuter [16] and Iglehart [10] analyze the competition process in terms of bivariate and multivariate Markov chains, respectively, and they obtain sufficient conditions for a competition process to be regular, positive recurrent, absorbed with certainty, and to have finite mean absorption times. A simplified version analyzed by Billard [3] assumes that each species can only decrease in number because of deaths caused, for example, by starvation, overcrowding, or removal in some form. A particular partitioning of the underlying matrix of coefficients, which is lower triangular, allows Billard [3] to derive the population size probabilities and moments with relative ease.

In a more general setting, we may cite the work by Cushing [5], Ellner [6], Gopalsamy [9], Jovanović and Vasilova [11, 19], Li and Smith [12, 13], Qi-Min et al. [15], and Zhang and Han [20], among others, who study a variety of models under stochastic and deterministic perspectives, such as age-dependent mortality and fertility functions (Gopalsamy [9]), age-structured models (Qi-Min et al. [15], Zhang and Han [20]), and four species that coexist in competition for three essential resources (Li and Smith [12]). Cushing [5] studies the Lotka-Volterra equations for two competing species under the assumption that the coefficients are periodic functions of a common period. Linear assumptions in Lotka-Volterra models for the interspecific interference are relaxed in Gilpin-Ayala models, recently analyzed by Jovanović and Vasilova [11, 19]. In the case of some models of two species competing in a randomly varying environment, Ellner [6] obtains sufficient conditions for convergence to the corresponding stationary distribution. Li and Smith [13] incorporate internal resource variables and external resource availability, and apply the resulting model to microbial growth on two essential limiting resources. Stochastic competition models have been recently applied in mathematical immunology as well. We may cite the work by Molina-París et al. [14], and Stirk et al. [18], where the dynamics of two competing T cell clonotypes are studied in terms of a bivariate competition process for the number of T cells belonging to the pair of clonotypes.

In this paper, the interest is in a stochastic model, termed Ridler-Rowe process [17] for a community of two mutually competing species, which is related to the two-species autonomous competitive model (Zeeman [21]). The Ridler-Rowe process amounts to a time-homogeneous continuous-time Markov chain (CTMC) defined on the quarter plane $\mathbb{N}_0 \times \mathbb{N}_0$, where transitions are allowed only to neighboring states, and it is related to an ecosystem of two species where no emigration or immigration is supposed to take place. In analyzing the size of the surviving species (Ridler-Rowe [17]), the quadratic form of the death rates makes the solution intractable from an analytical point of view. Ridler-Rowe [17] approximates the behavior of the underlying process, as the initial popula-

tion size becomes large, by an essentially deterministic motion with a random diffusion of smaller order superimposed upon it. This approach leads Ridler-Rowe [17] to the asymptotic distribution of the size of the surviving species, and a limit result for the probability that a given species should survive the other. The approximation of Ridler-Rowe [17] depends only on the death rates and, consequently, it alone may not answer all the questions which might be reasonable to be asked about the extinction time, and about the joint distribution of the extinction time and the size of the surviving species, particularly under the assumption of small or moderate initial population sizes. Gómez-Corral and López García [7] present an alternative approach that incorporates the birth rates into modeling aspects and is amenable to numerical calculation. Such an approach is based on the use of percentiles of the maximum number of individuals alive in the ecosystem, and it is shown that it works specially as the initial size is small. The approach in [7] results in the replacement of the underlying Markov chain by a suitably defined finite CTMC; a comparative study between the asymptotic result of Ridler-Rowe [17], results obtained from a simulation study of the process, and the finite CTMC can be found in [7, Section 4]. The maximum size distribution also allows Gómez-Corral and López García [8] to investigate the joint distribution of the extinction size and the numbers of births and deaths occurring during an extinction cycle, as well as the effects of the killing strategy on the survival of an individual when random and age-dependent assignments are taken into account.

The purpose of this paper is to complement the treatment of the Ridler-Rowe process by focusing here on the residual lifetime of an individual, and the number of direct descendants under the assumption of various killing and reproductive strategies. To begin with, we define in Section 2 the underlying Markov chain model, which is formulated as a reducible CTMC over $\mathbb{N}_0 \times \mathbb{N}_0$ with the single absorbing state $(0, 0)$. In Section 3, we first define age-dependent killing strategies in terms of the way individuals within each species are selected to die. Iterative schemes for the Laplace-Stieltjes transforms of the residual lifetime and their moments are then derived following first-step principles. In Section 4, the distribution of the number of descendants is analyzed under various killing and reproductive strategies, and numerical examples in Section 5 are presented to show the influence of the killing and reproductive strategies on the dynamics of the competition process under different ecosystem conditions. For ease of reference, we summarize in Appendix A some of the matrix notation that is used in the paper, and Appendix B contains some algorithmic solutions.

2. The Markov chain model

The dynamics of the Ridler-Rowe process [17] are described in terms of a time-homogeneous CTMC $\mathcal{X} = \{(M(t), N(t)) : t \geq 0\}$ defined on the state space $\mathcal{S} = \mathbb{N}_0 \times \mathbb{N}_0$, where $M(t)$ and $N(t)$ are the numbers of individuals in species 1 and species 2, respectively, alive at time t . The process \mathcal{X} is uniquely specified by the following non-null transition rates $q_{(m,n),(m',n')}$ (Figure 1):

(i) For states (m, n) with $m > 0$ and $n > 0$,

$$q_{(m,n),(m',n')} = \begin{cases} \alpha_1 m, & \text{if } (m', n') = (m+1, n), \\ \beta_1 n, & \text{if } (m', n') = (m, n+1), \\ \gamma mn, & \text{if } (m', n') = (m-1, n), \\ \delta mn, & \text{if } (m', n') = (m, n-1), \end{cases} \quad (1)$$

and $q_{(m,n)} = -q_{(m,n),(m,n)} = (\alpha_1 + \gamma n)m + (\beta_1 + \delta m)n$, where $\alpha_1, \beta_1, \gamma$ and δ are strictly positive.

(ii) For states $(m, 0)$ with $m > 0$,

$$q_{(m,0),(m',n')} = \begin{cases} \alpha_1 m, & \text{if } (m', n') = (m+1, 0), \\ \alpha_2 m, & \text{if } (m', n') = (m-1, 0), \end{cases} \quad (2)$$

and $q_{(m,0)} = -q_{(m,0),(m,0)} = (\alpha_1 + \alpha_2)m$, with $\alpha_2 > 0$.

(iii) For states $(0, n)$ with $n > 0$,

$$q_{(0,n),(m',n')} = \begin{cases} \beta_1 n, & \text{if } (m', n') = (0, n+1), \\ \beta_2 n, & \text{if } (m', n') = (0, n-1), \end{cases} \quad (3)$$

and $q_{(0,n)} = -q_{(0,n),(0,n)} = (\beta_1 + \beta_2)n$, with $\beta_2 > 0$.

Equations (2) and (3) mean that, after one of the species first becomes extinct, the dynamics of \mathcal{X} can be readily studied from well-known results on birth-and-death processes defined on $\mathbb{N}_0 \times \{0\}$ (extinction of species 2) and $\{0\} \times \mathbb{N}_0$ (extinction of species 1), where $(0, 0)$ is an absorbing state. If, for instance, species 2 becomes extinct and the size of the surviving species equals $m_0 \geq 1$ at time $T = \inf\{t : \text{either } M(t) = 0 \text{ or } N(t) = 0\}$, then species 1 evolving after T behaves as a birth-and-death process on $\mathbb{N}_0 \times \{0\}$ with birth rates $\{\alpha_1 m : m \geq 0\}$ and death rates $\{\alpha_2 m : m \geq 1\}$. As a result, species 1 becomes extinct (Allen [1, Theorems 6.2-6.3]) with probability one if $\alpha_2 \geq \alpha_1$, and with probability $(\alpha_1^{-1} \alpha_2)^{m_0}$ if $\alpha_2 < \alpha_1$.

If we denote $\mathcal{C}_0^1 = \{(m, 0) : m \geq 1\}$ and $\mathcal{C}_0^2 = \{(0, n) : n \geq 1\}$, then we may write down

$$\mathcal{S} = \mathcal{C} \cup \mathcal{C}_0^1 \cup \mathcal{C}_0^2 \cup \{(0, 0)\},$$

where $\mathcal{C} = \mathbb{N} \times \mathbb{N}$ is an irreducible class of transient states. Suppose that states are labeled so that states in \mathcal{C} precede those in \mathcal{C}_0^1 , states in \mathcal{C}_0^1 precede those in \mathcal{C}_0^2 , and states in \mathcal{C}_0^2 precede the absorbing state $(0, 0)$. Then, the infinitesimal generator \mathbf{Q} of \mathcal{X} takes the form

$$\mathbf{Q} = \begin{pmatrix} \mathbf{T} & \mathbf{S}_1 & \mathbf{S}_2 & \mathbf{0} \\ \mathbf{0} & \mathbf{T}_1 & \mathbf{0} & \alpha_2 \mathbf{e}(1) \\ \mathbf{0} & \mathbf{0} & \mathbf{T}_2 & \beta_2 \mathbf{e}(1) \\ \mathbf{0}^T & \mathbf{0}^T & \mathbf{0}^T & 0 \end{pmatrix},$$

where \mathbf{T}_1 and \mathbf{T}_2 are related to two suitably defined birth-and-death processes over $\mathcal{C}_0^1 \cup \{(0, 0)\}$ and $\mathcal{C}_0^2 \cup \{(0, 0)\}$, respectively, and \mathbf{T} , \mathbf{S}_1 and \mathbf{S}_2 are structured sub-matrices. Specifically, \mathbf{S}_1 and \mathbf{S}_2 correspond to jumps from the class \mathcal{C} of transient states to the sub-sets \mathcal{C}_0^1 and \mathcal{C}_0^2 , respectively, while \mathbf{T} corresponds to jumps between states in the class \mathcal{C} . By expressing the class \mathcal{C} as $\cup_{k=2}^{\infty} l(k)$ with the k th level defined by $l(k) = \{(m, n) \in \mathcal{S} : m + n = k, m > 0, n > 0\}$, we may express the sub-matrix \mathbf{T} in the form

$$\mathbf{T} = \begin{pmatrix} \mathbf{B}_{2,2} & \mathbf{B}_{2,3} & & & \\ \mathbf{B}_{3,2} & \mathbf{B}_{3,3} & \mathbf{B}_{3,4} & & \\ & \mathbf{B}_{4,3} & \mathbf{B}_{4,4} & \mathbf{B}_{4,5} & \\ & & \ddots & \ddots & \ddots \end{pmatrix}, \quad (4)$$

where $\mathbf{B}_{k,k}$ is a diagonal matrix of order $k - 1$ with i th entry $-q_{(k-i,i)}$, and the entries of $\mathbf{B}_{k,k'}$ are associated with jumps from states of the k th level to states of the k' th level, for $k' \in \{k - 1, k + 1\}$; see Appendix A for concrete specifications of the matrices $\mathbf{B}_{k,k-1}$, $\mathbf{B}_{k,k+1}$, \mathbf{S}_1 , \mathbf{S}_2 , \mathbf{T}_1 and \mathbf{T}_2 .

The assumptions made on the transition rates $q_{(m,n),(m',n')}$ as functions of m and n guarantee (Gómez-Corral and López García [7, Appendix], Reuter [16, Theorem 5]) that the extinction of one or other species occurs with probability one, and the expectation of the time at which this species first becomes extinct is finite regardless of the initial population size $(m, n) \in \mathcal{C}$. In Sections 3 and 4, we focus on an individual belonging to species 1, and study its residual lifetime and the number of direct descendants. The behavior of this individual is analyzed under the practically relevant situation when $\alpha_2 \geq \alpha_1$, which guarantees that the final extinction of species 1 is certain.

3. Residual lifetime

Let us assume that, at time $t = 0$, we mark an individual in species 1. In studying the residual lifetime of this *marked* individual, we have to specify the way individuals of species 1 are selected to die. We define a killing strategy as a family of mass functions $\mathcal{K} = \{\mathbf{s}_m : m \geq 1\}$, where the mass function \mathbf{s}_m is given by $\mathbf{s}_m = \{s_m(a) : 1 \leq a \leq m\}$ and the value $s_m(a)$ determines the probability that, as a death within species 1 occurs, the a th youngest individual in species 1 dies, given that species 1 consists of $m \geq 1$ individuals at that particular time instant. A natural killing strategy is specified by $\mathbf{s}_m \sim \text{Binomial}(m - 1, p_s)$ with $p_s \in [0, 1]$, where the probabilities $s_m(a)$ are given by

$$s_m(a) = \binom{m-1}{a-1} p_s^{a-1} (1-p_s)^{m-a},$$

for ages $a \in \{1, 2, \dots, m\}$; in this case, the values $p_s = 0$ and 1 yield the youngest-order and the oldest-order assignments¹, respectively, and values of p_s

¹Basic killing strategies are as follows: (i) *random-order assignment* (there exists identical chance for selecting the individual who dies), with values $s_m(a) = m^{-1}$ for $1 \leq a \leq m$,

with $0 < p_s < 0.5$ and $0.5 < p_s < 1$ reflect that younger and older individuals die more frequently, respectively.

For a predetermined killing strategy \mathcal{K} , we reformulate states (m, n) of the process \mathcal{X} by adding a third component a that amounts to the age of the marked individual within species 1. This results in states (m, n, a) for an ecosystem with m and n individuals in species 1 and 2, respectively, where the value $a = 0$ is related to the death of the marked individual. This leads us to consider an *augmented* version of \mathcal{X} , which is defined on the state space

$$\mathcal{S}^{(A)} = \mathcal{C}^{(A)} \cup \mathcal{C}_0^{(A),1} \cup \mathcal{C}_0^{(A),2} \cup \{(0, 0, 0)\},$$

where

$$\begin{aligned} \mathcal{C}^{(A)} &= \{(m, n, a) : (m, n) \in \mathcal{C}, 0 \leq a \leq m\}, \\ \mathcal{C}_0^{(A),1} &= \{(m, 0, a) : m \geq 1, 0 \leq a \leq m\}, \\ \mathcal{C}_0^{(A),2} &= \{(0, n, 0) : n \geq 1\}, \end{aligned}$$

and states in the sub-set $\{(m, n, 0) : (m, n) \in \mathcal{C} \cup \mathcal{C}_0^1\} \cup \mathcal{C}_0^{(A),2} \cup \{(0, 0, 0)\}$ are considered as absorbing. We remark that absorbing states in $\mathcal{S}^{(A)}$ represent the death of the marked individual under study. Figure 2 shows transitions between augmented states, for initial states $(m, n, a) \in \mathcal{C}^{(A)}$ and $(m, 0, a) \in \mathcal{C}_0^{(A),1}$ with $1 \leq a \leq m$. For later use, we define the values $s_m(< a)$ and $s_m(> a)$ as $s_m(< a) = \sum_{a'=1}^{a-1} s_m(a')$ and $s_m(> a) = \sum_{a'=a+1}^m s_m(a')$, with $s_m(< 1) = s_m(> m) = 0$.

For the marked individual, we define its residual lifetime in terms of the following random variables:

$T_{(m,n,a)}$ is the residual lifetime of the marked individual if species 1 and 2 consist of $m > 0$ and n individuals, respectively, and the age of the marked individual at time $t = 0$ is given by $a \in \{1, 2, \dots, m\}$.

Then, it is readily seen that the Laplace-Stieltjes transforms $\phi_{(m,n,a)}(\theta) = E[\exp\{-\theta T_{(m,n,a)}\}]$, for $Re(\theta) \geq 0$, satisfy

(i) For states (m, n, a) with $1 \leq a \leq m$ and $n \geq 1$,

$$\begin{aligned} &(\theta + (\alpha_1 + \gamma n)m + (\beta_1 + \delta m)n) \phi_{(m,n,a)}(\theta) \\ &= \alpha_1 m \phi_{(m+1,n,a+1)}(\theta) + \beta_1 n \phi_{(m,n+1,a)}(\theta) \\ &+ \gamma m n (s_m(< a) \phi_{(m-1,n,a-1)}(\theta) + s_m(a) + s_m(> a) \phi_{(m-1,n,a)}(\theta)) \\ &+ \delta m n \phi_{(m,n-1,a)}(\theta). \end{aligned} \tag{5}$$

that is, $\mathbf{s}_m \sim \text{Uniform}\{1, 2, \dots, m\}$; (ii) *the-oldest-order assignment* (the oldest individual dies whenever a death occurs), with values $s_m(a) = \delta_{a,m}$ for $1 \leq a \leq m$; and (iii) *the youngest-order assignment* (the youngest individual dies whenever a death occurs), with values $s_m(a) = \delta_{1,a}$ for $1 \leq a \leq m$.

(ii) For states $(m, 0, a)$ with $1 \leq a \leq m$,

$$\begin{aligned} (\theta + (\alpha_1 + \alpha_2)m) \phi_{(m,0,a)}(\theta) &= \alpha_1 m \phi_{(m+1,0,a+1)}(\theta) \\ &+ \alpha_2 m (s_m(< a) \phi_{(m-1,0,a-1)}(\theta) + s_m(a) + s_m(> a) \phi_{(m-1,0,a)}(\theta)). \end{aligned} \quad (6)$$

It should be pointed out here that, since every absorbing state in the augmented process amounts to the death of the marked individual, Laplace-Stieltjes transforms for these states are all equal to 1, and they behave as boundary conditions in (5)-(6). Similarly to [8, Equations (4)-(7)], (5)-(6) result in a theoretical solution that is not amenable to numerical implementation. Therefore, we adopt a truncation procedure that, for large enough values K and K' with $K-1 \leq K'$, examines the dynamics of \mathcal{X} till absorption into the absorbing state $(0, 0)$ but under the restriction that the finite set of states

$$\begin{aligned} \mathcal{S}(K; K') &= \bigcup_{k=2}^K l(k) \cup \{(m, 0) : 1 \leq m \leq K'\} \cup \{(0, n) : 1 \leq n \leq K-1\} \\ &\cup \{(0, 0)\} \end{aligned}$$

cannot be abandoned. For the initial state $(m, n) \in \mathcal{C}$, this procedure involves truncation to a finite matrix $\mathbf{Q}(K, K')$, and constructing a sequence of *restricted* Laplace-Stieltjes transforms of $T_{(m,n,a)}$ on the set $A_{(m,n)}^q$ of sample paths verifying that the process \mathcal{X} does not leave the sub-set $\mathcal{S}(K; K')$; note that the value q in $A_{(m,n)}^q$ is closely related to the selection of K and K' in Remark 1, where the effects of overpopulation in the ecosystem are taken into account.

Remark 1 In our approach, values K and K' are inherently linked to the initial state $(m, n) \in \mathcal{C}$. They are specified as follows:

Step 1 We select K as the $(100q)$ th percentile K_q of $X_{\max}^{(m,n)}$, where $X_{\max}^{(m,n)}$ is the maximum number of individuals simultaneously alive during an extinction cycle starting with m and n individuals in species 1 and 2, respectively. Then, for a predetermined probability $q \in (0, 1)$, the value $K = K_q$ is routinely evaluated from [7, Algorithm 1].

Step 2 We initialize $K' = K - 1$ and progressively increase K' until $p(m, n) = P(A_{(m,n)}^q) > q$. This means that the probability of leaving the finite set $\mathcal{S}(K; K')$ of states is as small as desired, by choosing $q \in (0, 1)$ large enough.

For an ecosystem consisting of $m > 0$ and $n > 0$ individuals in species 1 and 2, the probability $p(m, n)$ in Step 2 (Remark 1) can be readily derived by solving a finite system of linear equations, which involve probabilities $p(m', n')$ for states $(m', n') \in \mathcal{S}(K; K')$; in particular, for states of the form $(m', 0)$, it is seen that $p(m', 0) = P(X_{\max}^{(m',0)} \leq K')$ and

$$P\left(X_{\max}^{(m',0)} \leq K'\right) = \frac{(\alpha_2/\alpha_1)^{K'-m'+1} - 1}{(\alpha_2/\alpha_1)^{K'+1} - 1} \left(\frac{\alpha_2}{\alpha_1}\right)^{m'}, \quad m' \leq K'. \quad (7)$$

In our numerical work (Section 5), the focus is on initial states $(m, n) \in \mathcal{C}$ in such a way that there exists real competition between species 1 and 2. However, if the initial state has the form $(m, 0)$, the truncating procedure can be appropriately adapted since there is no need of the truncating value K any more. More concretely, the process \mathcal{X} starting from $(m, 0)$ behaves as a birth-and-death process over $\mathcal{C}_0^1 \cup \{(0, 0)\}$ and, consequently, the truncating procedure in Step 2 (Remark 1) starting with $K' = n$ is still valid; in this case, it is clear that $p(m, 0) = P(X_{\max}^{(m,0)} \leq K')$.

Once the values K and K' are in hand, we replace the original process \mathcal{X} by its restriction to the set $A_{(m,n)}^q$ of sample paths. We recall that, by Remark 1, values K and K' depend on the initial state $(m, n) \in \mathcal{C}$ and the probability $q \in (0, 1)$. Then, we propose to estimate the *true* Laplace-Stieltjes transform $\phi_{(m,n,a)}(\theta)$ by the *restricted* transform

$$\phi_{(m,n,a)}(\theta; q) = E \left[\exp\{-\theta T_{(m,n,a)}\}; A_{(m,n)}^q \right], \quad \operatorname{Re}(\theta) \geq 0.$$

It is worth noting that, by Remark 1, this implies that $\phi_{(m,n,a)}(0; q) > q$ since $p(m, n) = \phi_{(m,n,a)}(0; q)$. For ease of notation, we from now on denote the restricted transform $\phi_{(m,n,a)}(\theta; q)$ by $\phi_{(m,n,a)}(\theta)$. It is seen that the restricted transforms satisfy a finite system of linear equations, which can be decomposed into two sub-systems: (a) Sub-system 1 involves states in the set $\bar{\mathcal{C}}_0^{(A),1} = \{(m, 0, a) : 1 \leq m \leq K', 1 \leq a \leq m\}$; and (b) Sub-system 2 is related to states (m, n, a) with $(m, n) \in \cup_{k=2}^K l(k)$ and $1 \leq a \leq m$, but it also involves some states of $\bar{\mathcal{C}}_0^{(A),1}$.

Sub-system 1 The first sub-system of equations is inherently connected to the dynamics of a finite birth-and-death process defined on $\{0, 1, \dots, K'\} \times \{0\}$, and it is derived from first-passage arguments. Specifically, it consists of the following equations:

$$\begin{aligned} (\theta + \alpha_1 + \alpha_2) \phi_{(1,0,1)}(\theta) &= \alpha_1 \phi_{(2,0,2)}(\theta) + \alpha_2, & (8) \\ (\theta + (\alpha_1 + \alpha_2)m) \phi_{(m,0,a)}(\theta) &= (1 - \delta_{m,K'}) \alpha_1 m \phi_{(m+1,0,a+1)}(\theta) \\ &+ \alpha_2 m (s_m(< a) \phi_{(m-1,0,a-1)}(\theta) + s_m(a) p(m-1, 0) \\ &+ s_m(> a) \phi_{(m-1,0,a)}(\theta)), \quad 2 \leq m \leq K', \quad 1 \leq a \leq m, & (9) \end{aligned}$$

where $p(m', n')$ denotes the probability (Remark 1) that the process \mathcal{X} does not leave the set $\mathcal{S}(K; K')$ before absorption into states of $\{(0, 0)\} \cup \{(0, n) : 1 \leq n \leq K-1\}$, when (m', n') is its initial state.

Then, we may derive Algorithm 1 for computing the restricted Laplace-Stieltjes transforms of the residual lifetime $T_{(m,0,a)}$, for $1 \leq a \leq m \leq K'$. Its proof is based on a forward elimination backward substitution solution suggested by Ciarlet [4, page 144].

Algorithm 1 Computation of the restricted Laplace-Stieltjes transforms of $T_{(m,0,a)}$, for states $(m, 0, a)$ with $1 \leq a \leq m \leq K'$

Step 1: $i := 0$;
 $m := 1$;
 $h_m^i(\theta) := \theta + \alpha_1 + \alpha_2$;
 $j_m^i(\theta) := \alpha_2$;
while $1 \leq m \leq K' - 1$, repeat
 $m := m + 1$;
 $h_m^i(\theta) := \theta + (\alpha_1 + \alpha_2)m - \alpha_1\alpha_2m(m-1)s_m(< m)(h_{m-1}^i(\theta))^{-1}$;
 $j_m^i(\theta) := \alpha_2m(s_m(< m)(h_{m-1}^i(\theta))^{-1}j_{m-1}^i(\theta) + s_m(m)p(m-1, 0))$;
 $\phi_{(K',0,K')}(\theta) := (h_{K'}^i(\theta))^{-1}j_{K'}^i(\theta)$;
while $m \geq 2$, repeat
 $m := m - 1$;
 $\phi_{(m,0,m)}(\theta) := (h_m^i(\theta))^{-1}(\alpha_1m\phi_{(m+1,0,m+1)}(\theta) + j_m^i(\theta))$.
Step 2: While $i < K' - 2$, repeat
 $i := i + 1$;
 $h_{i+1}^i(\theta) := \theta + (\alpha_1 + \alpha_2)(i + 1)$;
 $j_{i+1}^i(\theta) := \alpha_2(i + 1)(s_{i+1}(1)p(i, 0) + s_{i+1>(> 1)\phi_{(i,0,1)}(\theta))$;
for $m = i + 2, i + 3, \dots, K'$, compute
 $h_m^i(\theta) := \theta + (\alpha_1 + \alpha_2)m$
 $- \alpha_1\alpha_2m(m-1)s_m(< m-i)(h_{m-1}^i(\theta))^{-1}$;
 $j_m^i(\theta) := \alpha_2m(s_m(< m-i)(h_{m-1}^i(\theta))^{-1}j_{m-1}^i(\theta)$
 $+ s_m(m-i)p(m-1, 0) + s_m(> m-i)\phi_{(m-1,0,m-i)}(\theta))$;
 $\phi_{(K',0,K'-i)}(\theta) := (h_{K'}^i(\theta))^{-1}j_{K'}^i(\theta)$;
for $m = K' - 1, K' - 2, \dots, i + 1$, compute
 $\phi_{(m,0,m-i)}(\theta) := (h_m^i(\theta))^{-1}(\alpha_1m\phi_{(m+1,0,m-i+1)}(\theta) + j_m^i(\theta))$.
Step 3: $h_{K'}^{K'-1}(\theta) := \theta + (\alpha_1 + \alpha_2)K'$;
 $j_{K'}^{K'-1}(\theta) := \alpha_2K'(s_{K'}(1)p(K' - 1, 0) + s_{K'}(> 1)\phi_{(K'-1,0,1)}(\theta))$;
 $\phi_{(K',0,1)}(\theta) := (h_{K'}^{K'-1}(\theta))^{-1}j_{K'}^{K'-1}(\theta)$.

For later use (Appendix A), we define the vector $\tilde{\mathbf{f}}^{(A)}(\theta)$, which contains the restricted Laplace-Stieltjes transforms $\phi_{(m,0,a)}(\theta)$ for augmented states $(m, 0, a)$ with $1 \leq a \leq m \leq K - 1$. In particular, $\tilde{\mathbf{f}}^{(A)}(\theta)$ consists of $K - 1$ sub-vectors $\tilde{\mathbf{f}}_m^{(A)}(\theta)$ whose a th entry is given by $\phi_{(m,0,a)}(\theta)$ for $1 \leq a \leq m \leq K - 1$.

Sub-system 2 To construct Sub-system 2, we first observe that (5) is satisfied by restricted transforms $\phi_{(m,n,a)}(\theta)$ for states $(1, n, 1)$ with $1 \leq n \leq K - 2$. For states (m, n, a) with $m \geq 2$, $n \geq 1$, $m + n < K$ and $1 \leq a \leq m$, it is readily seen that

$$\begin{aligned}
& (\theta + (\alpha_1 + \gamma n)m + (\beta_1 + \delta m)n) \phi_{(m,n,a)}(\theta) \\
&= \alpha_1 m \phi_{(m+1,n,a+1)}(\theta) + \beta_1 n \phi_{(m,n+1,a)}(\theta) \\
&+ \gamma mn (s_m(< a)\phi_{(m-1,n,a-1)}(\theta) + s_m(a)p(m-1, n) \\
&+ s_m(> a)\phi_{(m-1,n,a)}(\theta)) + \delta mn \phi_{(m,n-1,a)}(\theta). \tag{10}
\end{aligned}$$

For states (m, n, a) with $m \geq 2$, $n \geq 1$, $m + n = K$ and $1 \leq a \leq m$, it is seen

and entries of $\mathbf{C}_{m,m'}^{l,l'}$ are specified in Appendix A.

Algorithm 2 is inspired from block-Gaussian elimination, and it indicates how one may solve (13) in terms of previously computed transforms $\phi_{(m,0,a)}(\theta)$ (Algorithm 1), which are stored in vector $\tilde{\mathbf{f}}^{(A)}(\theta)$.

Algorithm 2 Computation of the restricted Laplace-Stieltjes transforms of $T_{(m,n,a)}$, for states (m,n,a) with $(m,n) \in \cup_{k=2}^K l(k)$ and $1 \leq a \leq m$

Step 1: $m := 1$;

$$\mathbf{H}_m(\theta) := \mathbf{I}_{m(K-m)} - \mathbf{C}_{m,m}^{(A)}(\theta);$$

$$\mathbf{J}_m(\theta) := \mathbf{c}_m^{(A)}(\theta);$$

while $m < K - 1$, repeat

$$m := m + 1;$$

$$\mathbf{H}_m(\theta) := \mathbf{I}_{m(K-m)} - \mathbf{C}_{m,m}^{(A)}(\theta) - \mathbf{C}_{m,m-1}^{(A)}(\theta)\mathbf{H}_{m-1}^{-1}(\theta)\mathbf{C}_{m-1,m}^{(A)}(\theta);$$

$$\mathbf{J}_m(\theta) := \mathbf{C}_{m,m-1}^{(A)}(\theta)\mathbf{H}_{m-1}^{-1}(\theta)\mathbf{J}_{m-1}(\theta) + \mathbf{c}_m^{(A)}(\theta).$$

Step 2: $\mathbf{f}_m^{(A)}(\theta) := \mathbf{H}_m^{-1}(\theta)\mathbf{J}_m(\theta)$;

while $m > 1$, repeat

$$m := m - 1;$$

$$\mathbf{f}_m^{(A)}(\theta) := \mathbf{H}_m^{-1}(\theta)(\mathbf{C}_{m,m+1}^{(A)}(\theta)\mathbf{f}_{m+1}^{(A)}(\theta) + \mathbf{J}_m(\theta)).$$

Let $\tau_{(m,n,a)}^{(l)}$ be the l th restricted moment of the residual lifetime $T_{(m,n,a)}$. In evaluating the restricted moments of the residual lifetime, straightforward algebra yields (8) and (9) with $\theta = 0$, where each transform $\phi_{(m,0,a)}(\theta)$ is replaced by its corresponding moment $\tau_{(m,0,a)}^{(l)}$, and α_2 (Equation (8)) and $\alpha_2 m s_m(a) p(m-1, 0)$ (Equation (9)) are replaced by $l\tau_{(1,0,1)}^{(l-1)}$ and $l\tau_{(m,0,a)}^{(l-1)}$, respectively; then, Algorithm B.1 (Appendix B) shows how to compute the expected values

$$\tau_{(m,0,a)}^{(l)} = E \left[T_{(m,0,a)}^l; A_{(m,0)}^a \right],$$

for states $(m,0,a)$ with $1 \leq a \leq m \leq K'$, by adapting our arguments in Algorithm 1. In a similar manner, Algorithm B.2 (Appendix B) computes the moments

$$\tau_{(m,n,a)}^{(l)} = E \left[T_{(m,n,a)}^l; A_{(m,n)}^a \right],$$

for states $(m,n,a) \in \bar{\mathcal{C}}^{(A)}$.

4. Number of direct descendants

In this section, we focus on a marked individual and evaluate the number of direct descendants, which aims to be a measure of the reproductive potential at a certain time instant. Let us assume that $t = 0$ is such a time instant, and define the number of next-generation births as follows:

$D_{(m,n,a)}$ is the number of direct descendants generated by a marked individual (in species 1) during its residual lifetime, on the assumption that m and n individuals in species 1 and 2, respectively, are alive at time $t = 0$ and the marked individual is the a th youngest one within species 1, with $1 \leq a \leq m$.

It is clear that the random variable $D_{(m,n,a)}$ depends on concrete specifications for the reproduction of individuals in species 1, as well as the killing strategy under consideration. In what follows we investigate its probability distribution (i.e., the probability mass function) in terms of generating functions

$$\varphi_{(m,n,a)}(z) = E[z^{D_{(m,n,a)}}], \quad |z| \leq 1,$$

and factorial moments

$$\nu_{(m,n,a)}^{(l)} = E[D_{(m,n,a)}(D_{(m,n,a)} - 1) \cdots (D_{(m,n,a)} - l + 1)],$$

for predetermined killing and reproductive strategies \mathcal{K} and \mathcal{R} , where the family $\mathcal{R} = \{\mathbf{r}_m : m \geq 1\}$ of mass functions is defined from the probabilities $r_m(a)$ that, as a birth within species 1 occurs, the a th youngest individual in species 1 is the progenitor, given that species 1 consists of $m \geq 1$ individuals, with $1 \leq a \leq m$.

As in the case of the residual lifetime $T_{(m,n,a)}$, the (infinite) system of linear equations governing the dynamics of the numbers $D_{(m,n,a)}$ of direct descendants is not analytically tractable and, consequently, the generating functions $\varphi_{(m,n,a)}(z)$ in our approach are estimated by the restricted versions on the set $A_{(m,n)}^q$ of sample paths, where $q \in (0, 1)$ is the large enough value chosen for selecting the truncating values K and K' ; see Remark 1 and (7). Then, the resulting finite system of linear equations can be decomposed into a first subsystem involving states in $\bar{\mathcal{C}}_0^{(A),1}$, and a second one for states (m, n, a) with $(m, n) \in \cup_{k=2}^K l(k)$ and $1 \leq a \leq m$, and some states of $\bar{\mathcal{C}}_0^{(A),1}$.

More concretely, a first-passage argument yields

$$\begin{aligned} (\alpha_1 + \alpha_2)\varphi_{(1,0,1)}(z) &= \alpha_1 z \varphi_{(2,0,2)}(z) + \alpha_2, & (15) \\ (\alpha_1 + \alpha_2)m\varphi_{(m,0,a)}(z) &= (1 - \delta_{m,K'})\alpha_1 m (r_m(a)z + r_m(\neq a))\varphi_{(m+1,0,a+1)}(z) \\ &\quad + \alpha_2 m (s_m(< a)\varphi_{(m-1,0,a-1)}(z) \\ &\quad + s_m(a)p(m-1,0) + s_m(> a)\varphi_{(m-1,0,a)}(z)), & (16) \\ &\quad 2 \leq m \leq K', 1 \leq a \leq m, \end{aligned}$$

where $r_m(\neq a) = 1 - r_m(a)$. Then, an appeal to [4, page 144] leads us to Algorithm 3.

Algorithm 3 Computation of the restricted generating functions of $D_{(m,0,a)}$, for states $(m, 0, a)$ with $1 \leq a \leq m \leq K'$

Step 1: $i := 0$;

$m := 1;$
 $\hat{h}_m^i(z) := (r_m(i)z + r_m(\neq i))^{-1} (\alpha_1 + \alpha_2);$
 $\hat{j}_m^i(z) := (r_m(i)z + r_m(\neq i))^{-1} \alpha_2;$
 while $1 \leq m \leq K' - 2$, repeat
 $m := m + 1;$
 $\hat{h}_m^i(z) := (r_m(m)z + r_m(\neq m))^{-1} \left((\alpha_1 + \alpha_2)m \right.$
 $\left. - \alpha_1 \alpha_2 m(m-1) s_m(< m) (\hat{h}_{m-1}^i(z))^{-1} \right);$
 $\hat{j}_m^i(z) := (r_m(m)z + r_m(\neq m))^{-1} \alpha_2 m$
 $\times \left(s_m(< m) (\hat{h}_{m-1}^i(z))^{-1} \hat{j}_{m-1}^i(z) + s_m(m) p(m-1, 0) \right);$
 $m := m + 1;$
 $\hat{h}_m^i(z) := (\alpha_1 + \alpha_2)m - \alpha_1 \alpha_2 m(m-1) (\hat{h}_{m-1}^i(z))^{-1} s_m(< m);$
 $\hat{j}_m^i(z) := \alpha_2 m \left(s_m(< m) (\hat{h}_{m-1}^i(z))^{-1} \hat{j}_{m-1}^i(z) + s_m(m) p(m-1, 0) \right);$
 $\varphi_{(m,0,m)}(z) := (\hat{h}_m^i(z))^{-1} \hat{j}_m^i(z);$
 while $2 \leq m \leq K'$, repeat
 $m := m - 1;$
 $\varphi_{(m,0,m)}(z) := (\hat{h}_m^i(z))^{-1} (\alpha_1 m \varphi_{(m+1,0,m+1)}(z) + \hat{j}_m^i(z)).$

Step 2: While $i < K' - 2$, repeat

$i := i + 1;$
 $\hat{h}_{i+1}^i(z) := (r_{i+1}(1)z + r_{i+1}(\neq 1))^{-1} (\alpha_1 + \alpha_2)(i + 1);$
 $\hat{j}_{i+1}^i(z) := (r_{i+1}(1)z + r_{i+1}(\neq 1))^{-1} \alpha_2(i + 1)$
 $\times (s_{i+1}(1)p(i, 0) + s_{i+1}(> 1)\varphi_{(i,0,1)}(z));$
 for $m = i + 2, i + 3, \dots, K' - 1$, compute
 $\hat{h}_m^i(z) := (r_m(m-i)z + r_m(\neq m-i))^{-1} \left((\alpha_1 + \alpha_2)m \right.$
 $\left. - \alpha_1 \alpha_2 m(m-1) s_m(< m-i) (\hat{h}_{m-1}^i(z))^{-1} \right);$
 $\hat{j}_m^i(z) := (r_m(m-i)z + r_m(\neq m-i))^{-1}$
 $\times \alpha_2 m \left(s_m(< m-i) (\hat{h}_{m-1}^i(z))^{-1} \hat{j}_{m-1}^i(z) \right.$
 $\left. + s_m(m-i)p(m-1, 0) + s_m(> m-i)\varphi_{(m-1,0,m-i)}(z) \right);$
 $\hat{h}_{K'}^i(z) := (\alpha_1 + \alpha_2)K' - \alpha_1 \alpha_2 K'(K'-1) s_{K'}(< K'-i) (\hat{h}_{K'-1}^i(z))^{-1};$
 $\hat{j}_{K'}^i(z) := \alpha_2 K' \left(s_{K'}(< K'-i) (\hat{h}_{K'-1}^i(z))^{-1} \hat{j}_{K'-1}^i(z) \right.$
 $\left. + s_{K'}(K'-i)p(K'-1, 0) + s_{K'}(> K'-i)\varphi_{(K'-1,0,K'-i)}(z) \right);$
 $\varphi_{(K',0,K'-i)}(z) := (\hat{h}_{K'}^i(z))^{-1} \hat{j}_{K'}^i(z);$
 for $m = K' - 1, K' - 2, \dots, i + 1$, compute
 $\varphi_{(m,0,m-i)}(z) := (\hat{h}_m^i(z))^{-1}$
 $\times \left(\alpha_1 m \varphi_{(m+1,0,m-i+1)}(z) + \hat{j}_m^i(z) \right);$
 $\varphi_{(K',0,1)}(z) := ((\alpha_1 + \alpha_2)K')^{-1} \alpha_2 K'$
 $\times \left(s_{K'}(1)p(K'-1, 0) + s_{K'}(> 1)\varphi_{(K'-1,0,1)}(z) \right).$

Similarly to (15)-(16), the restricted generating functions $\varphi_{(m,n,a)}(z)$ for states (m, n, a) with $(m, n) \in \cup_{k=2}^K l(k)$ and $1 \leq a \leq m$, satisfy the equalities

$$\begin{aligned} (\alpha_1 + \gamma n + (\beta_1 + \delta)n)\varphi_{(1,n,1)}(z) &= (1 - \delta_{n,K-1}) \\ &\times (\alpha_1 z \varphi_{(2,n,2)}(z) + \beta_1 n \varphi_{(1,n+1,1)}(z)) + \gamma n + \delta n \varphi_{(1,n-1,1)}(z), \\ &1 \leq n \leq K-1, \end{aligned} \quad (17)$$

$$\begin{aligned} ((\alpha_1 + \gamma n)m + (\beta_1 + \delta m)n)\varphi_{(m,n,a)}(z) &= \alpha_1 m(r_m(a)z + r_m(\neq a))\varphi_{(m+1,n,a+1)}(z) + \beta_1 n \varphi_{(m,n+1,a)}(z) \\ &+ \gamma mn \left(s_m(< a)\varphi_{(m-1,n,a-1)}(z) + s_m(a)p(m-1, n) \right. \\ &\left. + s_m(> a)\varphi_{(m-1,n,a)}(z) \right) + \delta mn \varphi_{(m,n-1,a)}(z), \\ &2 \leq m \leq K-1, n \geq 1, m+n < K, 1 \leq a \leq m, \end{aligned} \quad (18)$$

$$\begin{aligned} ((\alpha_1 + \gamma n)m + (\beta_1 + \delta m)n)\varphi_{(m,n,a)}(z) &= \gamma mn (s_m(< a)\varphi_{(m-1,n,a-1)}(z) \\ &+ s_m(a)p(m-1, n) + s_m(> a)\varphi_{(m-1,n,a)}(z)) + \delta mn \varphi_{(m,n-1,a)}(z), \\ &2 \leq m \leq K-1, n \geq 1, m+n = K, 1 \leq a \leq m. \end{aligned} \quad (19)$$

In matrix form, Equations (17)-(19) can be written as

$$\begin{aligned} \mathbf{g}_m(z) &= (1 - \delta_{1,m})\mathbf{C}_{m,m-1}^{(A)}(0)\mathbf{g}_{m-1}(z) + \mathbf{C}_{m,m}^{(A)}(0)\mathbf{g}_m(z) \\ &+ (1 - \delta_{m,K'-1})\hat{\mathbf{C}}_{m,m+1}(z)\mathbf{g}_{m+1}(z) + \hat{\mathbf{c}}_m(z), \quad 1 \leq m \leq K-1, \end{aligned}$$

where $\mathbf{g}_m(z)$ consists of sub-vectors $\mathbf{g}_m^a(z)$ and the n th entry of $\mathbf{g}_m^a(z)$ is given by $\varphi_{(m,n,a)}(z)$, for $1 \leq a \leq m \leq K-1$ and $1 \leq n \leq K-m$. The matrix $\hat{\mathbf{C}}_{m,m+1}(z)$ has the structured form

$$\begin{pmatrix} \mathbf{0}_{(K-m) \times (K-m-1)} & \hat{\mathbf{C}}_{m,m+1}^{1,2}(z) & & & \\ & & \hat{\mathbf{C}}_{m,m+1}^{2,3}(z) & & \\ & & & \ddots & \\ & & & & \hat{\mathbf{C}}_{m,m+1}^{m,m+1}(z) \end{pmatrix}, \quad (20)$$

with sub-matrices $\hat{\mathbf{C}}_{m,m+1}^{a,a+1}(z) = (r_m(a)z + r_m(\neq a))\mathbf{C}_{m,m+1}^{a,a+1}(0)$, and the vector $\hat{\mathbf{c}}_m(z)$ is specified by

$$\hat{\mathbf{c}}_m(z) = \mathbf{A}^{(A)}(0)\tilde{\mathbf{g}}_m(z) + \mathbf{t}^{(A)}(0),$$

where the a th entry of $\tilde{\mathbf{g}}_m(z)$ is given by $\varphi_{(m,0,a)}(z)$. As the reader may easily verify, Algorithm 2 allows us to compute the restricted solution $\mathbf{g}_m(z)$ by replacing $\mathbf{C}_{m,m'}^{(A)}(\theta)$, $\mathbf{C}_{m,m+1}^{(A)}(\theta)$ and $\mathbf{c}_m^{(A)}(\theta)$ by $\mathbf{C}_{m,m'}^{(A)}(0)$, $\hat{\mathbf{C}}_{m,m+1}(z)$ and $\hat{\mathbf{c}}_m(z)$, for $m' \in \{m-1, m\}$.

Algorithms B.3-B.4 (Appendix B) show how to compute the restricted factorial moments of the number of descendants, for augmented states (m, n, a) in $\mathcal{S}^{(A)}$. The correlation structure between the residual lifetime $T_{(m,n,a)}$ and the number $D_{(m,n,a)}$ of descendants may be analyzed by using the joint transform

$$E [\exp\{-\theta T_{(m,n,a)}\} z^{D_{(m,n,a)}}], \quad \text{Re}(\theta) \geq 0, |z| \leq 1,$$

which can be estimated by its restricted version on the set $A_{(m,n)}^q$ of sample paths. For practical use, this means that the restricted joint transforms of the random pairs $(T_{(m,n,a)}, D_{(m,n,a)})$, for augmented states in $\mathcal{S}^{(A)}$, can be characterized as the solution of a finite system of linear equations, and the coefficient of correlation $\rho(T_{(m,n,a)}, D_{(m,n,a)})$ may be readily derived by taking derivatives on the resulting equations at point $(\theta, z) = (0, 1)$. It is clear that Sub-systems 1-2 (Section 3) and Equations (15)-(19) can be then viewed as particular cases of the resulting system of equations at points (θ, z) with $z = 1$ and $Re(\theta) \geq 0$, and $\theta = 0$ and $|z| \leq 1$, respectively. For the sake of brevity, we omit the details.

5. Numerical examples

Next we present a numerical study of our preceding theoretical results which illustrates the effect of the killing and reproductive strategies \mathcal{K} and \mathcal{R} on the residual lifetime and the number of descendants. In our examples, we consider an ecosystem with *balanced* competition between species 1 and 2 and, more concretely, per capita parameters are selected as $(\alpha_1, \gamma) = (\beta_1, \delta) = (1.0, 0.25)$, and $\alpha_2 = 1.25$. Initial population sizes in Figures 3-10 are given by $(m, n) = (20, 10)$, $(20, 20)$ and $(20, 30)$, and they should be considered as slowly, moderately or highly competitive ecosystems, respectively, for an individual belonging to species 1.

Our examples in Figures 3 and 4 are related to the residual lifetime of a marked individual, for killing strategies based on Binomial and Uniform families. Specifically, Figures 3 and 4 show the variability of the expected value and the coefficient of variation as functions of the killing probability p_s , for ecosystems with initial sizes $(m, n) = (20, 10)$, $(20, 20)$ and $(20, 30)$. In each graph, three curves associated with the Binomial case and initial ages $a \in \{5, 10, 15\}$ are displayed; the solid line is related to the Uniform case, and it does not depend on p_s . It is worth noting that smaller values of the expected residual lifetime are associated with more overcrowded ecosystems at the initial time instant, regardless of the killing strategy. This reveals that the effect of the killing strategy on the expected residual lifetime decreases with increasing initial sizes, thus showing the influence of an increasing *environmental pressure*. We also observe that, as is to be expected, the expected residual lifetime behaves as an increasing function of the initial age for small values of p_s and, on the contrary, it decreases with increasing values of the initial age for higher values of the killing probability p_s . This behavior can be easily explained by recalling that, in the Binomial case, the values of p_s varying in $[0, 0.5)$ and $(0.5, 1]$ reflect that younger individuals and older individuals will die more frequently, respectively. Values of p_s that are close to 0.5 do not yield any remarkable behavior on the expected residual lifetime of the marked individual, which is inherently linked to the fact that killing strategies are *dynamically* adapted over time as a function of the number $M(t)$ of individuals alive in species 1.

The coefficient of variation is a dimensionless number, so when comparing between two values of p_s yielding significantly different expected values (Figure

3), it is observed in Figure 4 that, for every fixed initial size (m, n) , the distribution of the residual lifetime shows slower-variance when the killing probability p_s is close to 1 and, consequently, the killing strategy approaches the oldest-order assignment. We point out here that, in the particular case $p_s = 1$ representing the oldest-order assignment, the residual lifetime of the marked individual with initial age a is exactly described by the time until occurring $m - a$ deaths within species 1, which yields low values for the coefficient of variation regardless of the initial state. Moreover, when we fix the initial population size (m, n) , the highest variance is attained at moderately small magnitudes of the killing probability p_s if the marked individual is young (Figure 4, initial age $a = 5$) at the initial time instant; on the contrary, moderately high values of p_s lead to higher variance when the initial age increases (Figure 4, $a = 15$).

In Figures 5-7, we focus on the mean number of descendants. Figures 5 and 6 serve to show the behavior of this mean value as a function of the killing probability p_s when a Binomial killing strategy is assumed; each graph contains a solid curve, which is related to the Uniform case, and five curves corresponding to Binomial reproductive strategies with probabilities $p_r \in \{0, 0.25, 0.5, 0.75, 1\}$. Figures 5-6 suggest that the way in which the individuals reproduce within species 1 (i.e., the reproductive strategy \mathcal{R}) is crucial or not for the mean number of descendants of a marked individual depending on the ecosystem characteristics. More concretely, under a low competitive environment (in our examples, $(m, n) = (20, 10)$) or when the individual has a high expected residual lifetime (for example, $p_s \in [0, 0.5)$ and $a = 15$ in Figure 6), the reproductive strategy plays an important role in the number of descendants to be expected, and large numbers of descendants might be reached. On the other hand, in a more competitive ecosystem (in our examples, $(m, n) = (20, 30)$) or when the individual has a low expected residual lifetime (for example, $p_s \in (0.5, 1]$ and $a = 15$ in Figure 6), the expected number of descendants is small regardless of the particular reproductive strategy under study.

Figure 7 shows the variability of the mean number of descendants as a function of the reproductive probability p_r for initial sizes $(m, n) = (20, 10)$, $(20, 20)$ and $(20, 30)$, when the Uniform killing strategy is assumed. In each graph, we plot four curves corresponding to the initial ages $a \in \{5, 10, 15\}$ and the Uniform reproductive case. It is observed that increasing initial sizes (m, n) result in decreasing mean numbers of descendants, regardless of the killing strategy. In the same manner than with the reproductive strategy in Figures 5-6, the effect of the killing strategy on the number of descendants in Figure 7 vanishes under highly competitive environments. For every fixed size, the mean number of descendants behaves as a non-monotone function of the killing probability p_r , in such a way that graphs have similar shapes in the Binomial reproductive case, but the resulting magnitudes are notably different; in particular, maximum values are derived when the marked individual has a moderately high age (Figure 7, $a = 15$) at the initial time instant and older individuals reproduce more frequently than younger individuals in species 1.

In Figures 3-7 we have analyzed the impact of the way in which individuals die within the ecosystem on the expected residual lifetime and the expected

number of descendants, this latter descriptor also being affected by the way in which individuals reproduce within species 1. At the same time, identified behaviors in those figures reflect a clear dependence between the residual lifetime of a marked individual and its number of descendants, this dependence seeming higher or lower depending on the environmental conditions. To probabilistically quantify this dependence we plot in Figures 8-10, for the same ecosystem characteristics than in Figures 5-7, the coefficient of correlation between the residual lifetime of a marked individual and the number of descendants. As intuition tells us, values of this descriptor are strictly positive, which means that decreasing (respectively, increasing) residual lifetimes imply decreasing (respectively, increasing) numbers of descendants. In particular, Figures 8-9 show that the coefficient of correlation is not necessarily a monotone function of the killing probability p_s , but the resulting magnitudes are notably different with p_s varying. A similar remark may be made for the linear dependence between $T_{(m,n,a)}$ and $D_{(m,n,a)}$ in Figure 10, where it is observed that maximum values of the coefficient of correlation are related to the highest value of the initial age in our examples ($a = 15$) as the reproductive probability p_r is high, and however the smallest age ($a = 5$) in the initial time instant yields the maximum linear dependence if the values of p_r are small and moderate.

Acknowledgments

Financial support for this work was provided by the Government of Spain (Ministry of Economy and Competitiveness) and the European Commission through the project MTM-2011-23864. M. López-García was also supported by The Leverhulme Trust through the project RPG-2012-772.

Appendix A

Glossary of notation

Throughout this paper, vectors are denoted by bold lowercase letters (like \mathbf{a}) and matrices are represented in bold uppercase (like \mathbf{A}). The transpose of \mathbf{A} is denoted by \mathbf{A}^T and, by default, vectors are column vectors. The column vectors of order i with all entries equal 1 and 0 are denoted by \mathbf{e}_i and $\mathbf{0}_i$, respectively. We denote by $\mathbf{e}_i(j)$ the column vector of order i such that all entries equal 0, except for the j th one which equals 1. If the number of entries of \mathbf{e}_i , $\mathbf{0}_i$ and $\mathbf{e}_i(j)$ is not finite, then we use the notation \mathbf{e} , $\mathbf{0}$ and $\mathbf{e}(j)$, respectively.

The identity matrix of order i is denoted by \mathbf{I}_i , $\mathbf{0}_{i \times j}$ denotes the null matrix of dimension $i \times j$, and \mathbf{I} and $\mathbf{0}$ denote the identity and null matrices, respectively, with an infinite number of rows and columns, so that $\mathbf{0}$ can represent either an infinite vector or an infinite matrix of zeros depending on context. The matrix $\text{diag}(a_1, \dots, a_k)$ has elements a_1, \dots, a_k along its diagonal and zeros elsewhere, even if the entries a_1, \dots, a_k are vectors or matrices.

The Kronecker delta $\delta_{i,j}$ is equal to 1 if $i = j$, and 0 if $i \neq j$. For a set \mathcal{A} of states and $x, y \in \mathcal{A}$, $\#\mathcal{A}$ denotes the cardinality of \mathcal{A} , and $x \propto y$ denotes that x precedes y .

and $\mathbf{a}_m^{(A)}(\theta; a) = (\theta + (\alpha_1 + \gamma)m + \beta_1 + \delta m)^{-1} \delta m \mathbf{e}_{K-m}(1)$. In a similar manner, $\mathbf{t}^{(A)}(\theta)$ consists of column vectors $\mathbf{t}_m^{(A)}(\theta)$, for $1 \leq m \leq K-1$, where

$$\mathbf{t}_m^{(A)}(\theta) = \begin{pmatrix} \mathbf{t}_m^{(A)}(\theta; 1) \\ \mathbf{t}_m^{(A)}(\theta; 2) \\ \vdots \\ \mathbf{t}_m^{(A)}(\theta; m) \end{pmatrix},$$

and entries of $\mathbf{t}_m^{(A)}(\theta; a)$ are related to the death of the marked individual, when species 1 consists of m individuals, that is, the n th entry of $\mathbf{t}_m^{(A)}(\theta; a)$ is given by

$$(\theta + (\alpha_1 + \gamma n)m + (\beta_1 + \delta m)n)^{-1} \gamma m n (\delta_{1,m} + (1 - \delta_{1,m}) s_m(a) p(m-1, n)),$$

for $1 \leq n \leq K-m$.

By (5) and (10)-(12), entries of $\mathbf{C}_{m,m'}^{l,l'}(\theta)$ are specified as follows:

(i) For $1 \leq a \leq m \leq K-1$,

$$\left(\mathbf{C}_{m,m}^{a,a}(\theta) \right)_{i,j} = \begin{cases} (\theta + (\alpha_1 + \gamma i)m + (\beta_1 + \delta m)i)^{-1} \delta m i, & \text{if } j = i-1, \\ (\theta + (\alpha_1 + \gamma i)m + (\beta_1 + \delta m)i)^{-1} \beta_1 i, & \text{if } j = i+1, \\ 0, & \text{otherwise,} \end{cases}$$

with $1 \leq i, j \leq K-m$.

(ii) For $2 \leq a \leq m \leq K-1$,

$$\left(\mathbf{C}_{m,m-1}^{a,a-1}(\theta) \right)_{i,j} = \begin{cases} (\theta + (\alpha_1 + \gamma i)m + (\beta_1 + \delta m)i)^{-1} \gamma m i s_m(< a), & \text{if } j = i, \\ 0, & \text{otherwise,} \end{cases}$$

with $1 \leq i \leq K-m$ and $1 \leq j \leq K-m+1$.

(iii) For $2 \leq m \leq K-1$ and $1 \leq a \leq m$,

$$\left(\mathbf{C}_{m,m-1}^{a,a}(\theta) \right)_{i,j} = \begin{cases} (\theta + (\alpha_1 + \gamma i)m + (\beta_1 + \delta m)i)^{-1} \gamma m i s_m(> a), & \text{if } j = i, \\ 0, & \text{otherwise,} \end{cases}$$

with $1 \leq i \leq K-m$ and $1 \leq j \leq K-m+1$.

(iv) For $1 \leq a \leq m \leq K-2$,

$$\left(\mathbf{C}_{m,m+1}^{a,a+1}(\theta) \right)_{i,j} = \begin{cases} (\theta + (\alpha_1 + \gamma i)m + (\beta_1 + \delta m)i)^{-1} \alpha_1 m, & \text{if } j = i, \\ 0, & \text{otherwise,} \end{cases}$$

with $1 \leq i \leq K-m$ and $1 \leq j \leq K-m-1$.

Appendix B

Algorithms B.1 and B.2

Algorithm B.1 allows us to compute the l th moments $\tau_{(m,0,a)}^{(l)}$ from the previously computed values $h_m^i(0)$ and $\phi_{(m,0,a)}(0)$ in Algorithm 1.

Algorithm B.1 Computation of $\tau_{(m,0,a)}^{(l)} = E[T_{(m,0,a)}^l; A_{(m,0)}^q]$ for states $(m, 0, a)$ with $1 \leq a \leq m \leq K'$

Step 1: $r := 0$;

for $1 \leq a \leq m \leq K'$, compute

$$\tau_{(m,0,a)}^{(r)} := \phi_{(m,0,a)}(0).$$

Step 2: While $r < l$, repeat

$r := r + 1$;

$m := 1$;

$$j_m^{0,(r)} := r\tau_{(m,0,m)}^{(r-1)};$$

while $m < K'$, repeat

$m := m + 1$;

$$j_m^{0,(r)} := \alpha_2 m s_m(< m)(h_{m-1}^0(0))^{-1} j_{m-1}^{0,(r-1)} + r\tau_{(m,0,m)}^{(r-1)};$$

$$\tau_{(K',0,K')}^{(r)} := (h_{K'}^0(0))^{-1} j_{K'}^{0,(r)};$$

while $m > 1$, repeat

$m := m - 1$;

$$\tau_{(m,0,m)}^{(r)} := (h_m^0(0))^{-1} (\alpha_1 m \tau_{(m+1,0,m+1)}^{(r)} + j_m^{0,(r)});$$

$i := 0$;

while $i < K' - 2$ repeat

$i := i + 1$;

$$j_{i+1}^{i,(r)} := \alpha_2 (i+1) s_{i+1}(> 1) \tau_{(i,0,1)}^{(r)} + r\tau_{(i+1,0,1)}^{(r-1)};$$

for $m = i + 2, i + 3, \dots, K'$, compute

$$j_m^{i,(r)} := \alpha_2 m (s_m(< m - i)(h_{m-1}^i(0))^{-1} j_{m-1}^{i,(r)} + s_m(> m - i) \tau_{(m-1,0,m-i)}^{(r)}) + r\tau_{(m,0,m-i)}^{(r-1)};$$

$$\tau_{(K',0,K'-i)}^{(r)} := (h_{K'}^i(0))^{-1} j_{K'}^{i,(r)};$$

for $m = K' - 1, K' - 2, \dots, i + 1$, compute

$$\tau_{(m,0,m-i)}^{(r)} := (h_m^i(0))^{-1} (\alpha_1 m \tau_{(m+1,0,m+1-i)}^{(r)} + j_m^{i,(r)});$$

$$\tau_{(K',0,1)}^{(r)} := ((\alpha_1 + \alpha_2)K')^{-1} (\alpha_2 K' s_{K'}(> 1) \tau_{(K'-1,0,1)}^{(r)} + r\tau_{(K',0,1)}^{(r-1)}).$$

Similarly to Equation (13), the vector $\tau^{(l)}$ in Algorithm B.2 consists of sub-vectors $\tau_m^{(l)}$ with (restricted) moments $E[T_{(m,n,a)}^l; A_{(m,n)}^q]$ for states $(m, n, a) \in \bar{\mathcal{C}}^{(A)}$. Again, matrices $\mathbf{H}_m(0)$ and vectors $\mathbf{f}_m^{(A)}(0)$ used in Algorithm B.2 are those ones obtained in Algorithm 2 when solving (13).

Algorithm B.2 Computation of $\tau_{(m,n,a)}^{(l)} = E[T_{(m,n,a)}^l; A_{(m,n)}^q]$ for states $(m, n, a) \in \bar{\mathcal{C}}^{(A)}$

Step 1: $r := 0$;
 $m := 0$;
 while $m < K - 1$, repeat
 $m := m + 1$;
 $\tau_m^{(r)} := \mathbf{f}_m^{(A)}(0)$.
 Step 2: While $r < l$, repeat
 $r := r + 1$;
 $\mathbf{J}_1^{(r)} := (-1)^r \mathbf{c}_1^{(r)}(0) + \sum_{i=1}^r \binom{r}{i} (-1)^i \left(\mathbf{C}_{1,1}^{(A),(i)}(0) \tau_1^{(r-i)} + \mathbf{C}_{1,2}^{(A),(i)}(0) \tau_2^{(r-i)} \right)$;
 for $m = 2, 3, \dots, K - 1$, compute
 $\mathbf{J}_m^{(r)} := (-1)^r \mathbf{c}_m^{(r)}(0) + \mathbf{C}_{m,m-1}^{(A)}(0) \mathbf{H}_{m-1}^{-1}(0) \mathbf{J}_{m-1}^{(r)}(0)$
 $+ \sum_{i=1}^r \binom{r}{i} (-1)^i \left(\mathbf{C}_{m,m-1}^{(A),(i)}(0) \tau_{m-1}^{(r-i)} + \mathbf{C}_{m,m}^{(A),(i)}(0) \tau_m^{(r-i)} \right)$
 $+ (1 - \delta_{m,K-1}) \mathbf{C}_{m,m+1}^{(A),(i)}(0) \tau_{m+1}^{(r-i)}$;
 $\tau_{K-1}^{(r)} := \mathbf{H}_{K-1}^{-1}(0) \mathbf{J}_{K-1}^{(r)}$;
 for $m = K - 2, K - 3, \dots, 1$, compute
 $\tau_m^{(r)} := \mathbf{H}_m^{-1}(0) \left(\mathbf{C}_{m,m+1}^{(A)}(0) \tau_{m+1}^{(r)} + \mathbf{J}_m^{(r)} \right)$.

The matrix $\mathbf{C}_{m,m'}^{(A),(i)}(0)$ corresponds to the i th derivative of $\mathbf{C}_{m,m'}^{(A)}(\theta)$ at $\theta = 0$.
 Based on the structured form of $\mathbf{C}_{m,m'}^{(A)}(\theta)$ in (14), its elements are specified by

$$\begin{aligned}
 \left(\mathbf{C}_{m,m}^{a,a,(r)}(0) \right)_{i,j} &= \begin{cases} ((\alpha_1 + \gamma i)m + (\beta_1 + \delta m)i)^{-(r+1)} (-1)^{-r} r! \delta m i, & \text{if } j = i - 1, \\ ((\alpha_1 + \gamma i)m + (\beta_1 + \delta m)i)^{-(r+1)} (-1)^{-r} r! \beta_1 i, & \text{if } j = i + 1, \\ 0, & \text{otherwise,} \end{cases} \\
 \left(\mathbf{C}_{m,m-1}^{a,a-1,(r)}(0) \right)_{i,j} &= \begin{cases} ((\alpha_1 + \gamma i)m + (\beta_1 + \delta m)i)^{-(r+1)} (-1)^{-r} r! \gamma m i s_m (< a), & \text{if } j = i, \\ 0, & \text{otherwise,} \end{cases} \\
 \left(\mathbf{C}_{m,m-1}^{a,a,(r)}(0) \right)_{i,j} &= \begin{cases} ((\alpha_1 + \gamma i)m + (\beta_1 + \delta m)i)^{-(r+1)} (-1)^{-r} r! \gamma m i s_m (> a), & \text{if } j = i, \\ 0, & \text{otherwise,} \end{cases} \\
 \left(\mathbf{C}_{m,m+1}^{a,a+1,(r)}(0) \right)_{i,j} &= \begin{cases} ((\alpha_1 + \gamma i)m + (\beta_1 + \delta m)i)^{-(r+1)} (-1)^{-r} r! \alpha_1 m, & \text{if } j = i, \\ 0, & \text{otherwise.} \end{cases}
 \end{aligned}$$

The vector $\mathbf{c}_m^{(r)}(0)$ in Step 2 (Algorithm B.2) satisfies

$$(-1)^r \mathbf{c}_m^{(r)}(0) = \sum_{r'=0}^r \binom{r}{r'} (-1)^{r'} \mathbf{A}_m^{(A),(r')}(0) \tilde{\mathbf{f}}_m^{(A),(r-r')}(0) + \mathbf{t}_m^{(A),(r)}(0),$$

where $\mathbf{A}_m^{(A),(r)}(0)$ consists of the sub-vectors

$$\mathbf{a}_m^{(A),(r)}(0; a) = (-1)^r r! ((\alpha_1 + \gamma)m + \beta_1 + \delta m)^{-(r+1)} \delta m \mathbf{e}_{K-m}(1),$$

for $1 \leq a \leq m \leq K - 1$, $\mathbf{t}_m^{(A),(r)}(0)$ contains sub-vectors $\mathbf{t}_m^{(A),(r)}(0; a)$ with elements

$$\begin{aligned}
 \left(\mathbf{t}_m^{(A),(r)}(0; a) \right)_i &= r! ((\alpha_1 + \gamma i)m + (\beta_1 + \delta m)i)^{-(r+1)} \\
 &\quad \times \gamma m i (\delta_{1,m} + (1 - \delta_{1,m}) s_m(a) p(m - 1, i)),
 \end{aligned}$$

for $1 \leq i \leq K - m$ and $1 \leq a \leq m \leq K - 1$, and $\tilde{\mathbf{f}}_m^{(A),(l)}$ is a column vector of order m , whose a th entry is given by $\tau_{(m,0,a)}^{(l)}$.

Algorithms B.3 and B.4

In Algorithm B.3 the values $\nu_{(m,0,a)}^{(l)}$ correspond to the (restricted) moments

$$\nu_{(m,0,a)}^{(l)} = E[D_{(m,0,a)}(D_{(m,0,a)} - 1) \dots (D_{(m,0,a)} - l + 1); A_{(m,0)}^q],$$

for states $(m, 0, a) \in \bar{\mathcal{C}}_0^{(A),1}$. For states $(m, n, a) \in \bar{\mathcal{C}}^{(A)}$, the values $\nu_{(m,n,a)}^{(l)}$ in Algorithm B.4 are defined by

$$\nu_{(m,n,a)}^{(l)} = E[D_{(m,n,a)}(D_{(m,n,a)} - 1) \dots (D_{(m,n,a)} - l + 1); A_{(m,n)}^q].$$

In Algorithm 4, the matrix $\hat{\mathbf{C}}_{m,m+1}^{(1)}(1)$ in Step 2 has the structured form (20) with the sub-matrices $\hat{\mathbf{C}}_{m,m+1}^{a,a+1}(z)$ replaced by $r_m(a)\mathbf{C}_{m,m+1}^{a,a+1}(0)$, and the matrix $\hat{\mathbf{H}}_m(1)$ is iteratively evaluated, similarly to $\mathbf{H}_m(\theta)$ in Algorithm 2, from

$$\hat{\mathbf{H}}_m(z) = \mathbf{I}_{m(K-m)} - \mathbf{C}_{m,m}^{(A)}(0) - (1 - \delta_{1,m})\mathbf{C}_{m,m-1}^{(A)}(0)\hat{\mathbf{H}}_{m-1}^{-1}(z)\hat{\mathbf{C}}_{m-1,m}(z).$$

Finally, the vector $\hat{\mathbf{c}}_m^{(l)}(1)$ is defined by $\mathbf{A}^{(A)}(0)\tilde{\nu}_m^{(l)}$, where $\tilde{\nu}_m^{(l)}$ is the sub-vector with entries $\nu_{(m,0,a)}^{(l)}$ for $1 \leq a \leq m$, which are derived from Algorithm B.3.

Algorithm B.3 Computation of $\nu_{(m,0,a)}^{(l)}$ for states $(m, 0, a)$ with $1 \leq a \leq m \leq K'$

Step 1: $r := 0$;

for $1 \leq a \leq m \leq K'$, compute

$$\nu_{(m,0,a)}^{(r)} := \varphi_{(m,0,a)}(1).$$

Step 2: While $r < l$, repeat

$r := r + 1$;

$m := 1$;

$$\hat{j}_m^{0,(r)} := r r_m(1) \alpha_1 \nu_{(m+1,0,m+1)}^{(r-1)};$$

while $m < K'$, repeat

$m := m + 1$;

$$\hat{j}_m^{0,(r)} := \alpha_2 m s_m(< m) (\hat{h}_{m-1}^0(1))^{-1} \hat{j}_{m-1}^{0,(r)}$$

$$+ (1 - \delta_{m,K'}) \alpha_1 m r r_m(m) \nu_{(m+1,0,m+1)}^{(r-1)};$$

$$\nu_{(K',0,K')}^{(r)} := (\hat{h}_{K'}^0(1))^{-1} \hat{j}_{K'}^{0,(r)};$$

while $m > 1$, repeat

$m := m - 1$;

$$\nu_{(m,0,m)}^{(r)} := (\hat{h}_m^0(1))^{-1} (\alpha_1 m \nu_{(m+1,0,m+1)}^{(r)} + \hat{j}_m^{0,(r)});$$

$i := 0$;

while $i < K' - 2$ repeat

$i := i + 1$;

$$\begin{aligned}
\hat{j}_{i+1}^{i,(r)} &:= \alpha_2(i+1)s_{i+1}(>1)\nu_{(i,0,1)}^{(r)} + \alpha_1 m r r_m(1)\nu_{(i+2,0,2)}^{(r-1)}; \\
\text{for } m = i+2, i+3, \dots, K', \text{ compute} \\
\hat{j}_m^{i,(r)} &:= \alpha_2 m (s_m(<m-i)(\hat{h}_{m-1}^i(1))^{-1} \hat{j}_{m-1}^{i,(r)} \\
&\quad + s_m(>m-i)\nu_{(m-1,0,m-i)}^{(r)}) \\
&\quad + (1 - \delta_{m,K'}) m \alpha_1 r r_m(m-i)\nu_{(m+1,0,m+1-i)}^{(r-1)}; \\
\nu_{(K',0,K'-i)}^{(r)} &:= (\hat{h}_{K'}^i(1))^{-1} \hat{j}_{K'}^{i,(r)}; \\
\text{for } m = K'-1, K'-2, \dots, i+1, \text{ compute} \\
\nu_{(m,0,m-i)}^{(r)} &:= (\hat{h}_m^i(1))^{-1} (\alpha_1 m \nu_{(m+1,0,m+1-i)}^{(r)} + \hat{j}_m^{i,(r)}); \\
\nu_{(K',0,1)}^{(r)} &:= ((\alpha_1 + \alpha_2)K')^{-1} \alpha_2 K' s_{K'}(>1)\nu_{(K'-1,0,1)}^{(r)}.
\end{aligned}$$

Algorithm B.4 Computation of $\nu_{(m,n,a)}^{(l)}$ for states $(m, n, a) \in \bar{\mathcal{C}}^{(A)}$

Step 1: $r := 0$;

$m := 0$;

while $m < K-1$, repeat

$m := m+1$;

$\nu_m^{(r)} := \mathbf{g}_m(1)$.

Step 2: While $r < l$, repeat

$r := r+1$;

$\hat{\mathbf{j}}_1^{(r)} := \hat{\mathbf{c}}_1^{(r)}(1) + l\hat{\mathbf{C}}_{1,2}^{(1)}(1)\nu_2^{(l-1)}$;

for $m = 2, 3, \dots, K-1$, compute

$\hat{\mathbf{J}}_m^{(r)} := \hat{\mathbf{c}}_m^{(r)}(1) + \mathbf{C}_{m,m-1}^{(A)}(0)\hat{\mathbf{H}}_{m-1}^{-1}(1)\hat{\mathbf{J}}_{m-1}^{(r)} + (1 - \delta_{m,K-1})l\hat{\mathbf{C}}_{m,m+1}^{(1)}(1)\nu_{m+1}^{(l-1)}$;

$\nu_{K-1}^{(r)} := \hat{\mathbf{H}}_{K-1}^{-1}(1)\hat{\mathbf{J}}_{K-1}^{(r)}$;

for $m = K-2, K-3, \dots, 1$, compute

$\nu_m^{(r)} := \hat{\mathbf{H}}_m^{-1}(1)(\hat{\mathbf{C}}_{m,m+1}(1)\nu_{m+1}^{(r)} + \hat{\mathbf{J}}_m^{(r)})$.

References

- [1] Allen LJS (2003) An Introduction to Stochastic Processes with Applications in Biology. Pearson Education, New Jersey.
- [2] Allen LJS (2007) An Introduction to Mathematical Biology. Pearson Education, New Jersey.
- [3] Billard L (1974) Competition between two species. Stochastic Processes and Their Applications 2: 391-398.
- [4] Ciarlet PG (1989) Introduction to Numerical Linear Algebra and Optimization. Cambridge University Press, Cambridge.
- [5] Cushing JM (1980) Two species competition in a periodic environment. Journal of Mathematical Biology 10: 385-400.
- [6] Ellner S (1989) Convergence to stationary distributions in two-species stochastic competition models. Journal of Mathematical Biology 27: 451-462.

- [7] Gómez-Corral A, López García M (2012) Extinction times and size of the surviving species in a two-species competition process. *Journal of Mathematical Biology* 64: 255-289.
- [8] Gómez-Corral A, López García M (2012) On the number of births and deaths during an extinction cycle, and the survival of a certain individual in a competition process. *Computers & Mathematics with Applications* 64: 236-259.
- [9] Gopalsamy K (1982) Age-specific coexistence in two-species competition. *Mathematical Biosciences* 61: 101-122.
- [10] Iglehart DL (1964) Multivariate competition processes. *Annals of Mathematical Statistics* 35: 350-361.
- [11] Jovanović M, Vasilova M (2013) Dynamics of non-autonomous stochastic Gilpin-Ayala competition model with time-varying delays. *Applied Mathematics and Computation* 219: 6946-6964.
- [12] Li B, Smith HL (2003) Periodic coexistence of four species competing for three essential resources. *Mathematical Biosciences* 184: 115-135.
- [13] Li B, Smith HL (2007) Global dynamics of microbial competition for two resources with internal storage. *Journal of Mathematical Biology* 55: 481-515.
- [14] Molina-París C, Lythe G, Stirk ER (2011) Multivariate competition processes: a model for two competing T cell clonotypes. In: *Mathematical Models and Immune Cell Biology*, Molina-París C and Lythe G (Eds.), Springer, pp. 187-205.
- [15] Qi-Min Z, Wen-An L, Zan-Kan N (2004) Existence, uniqueness and exponential stability for stochastic age-dependent population. *Applied Mathematics and Computation* 154: 183-201.
- [16] Reuter GEH (1961) Competition processes. In: Neyman J (Ed.), *Proceedings of the 4th Berkeley Symposium on Mathematical Statistics and Probability, Vol. II: Contributions to Probability Theory*. University of California Press, Berkeley, pp. 421-430.
- [17] Ridler-Rowe CJ (1978) On competition between two species. *Journal of Applied Probability* 15: 457-465.
- [18] Stirk ER, Lythe G, van den Berg HA, Molina-París C (2010) Stochastic competitive exclusion in the maintenance of the naïve T cell repertoire. *Journal of Theoretical Biology* 265: 396-410.
- [19] Vasilova M, Jovanović M (2011) Stochastic Gilpin-Ayala competition model with infinite delay. *Applied Mathematics and Computation* 217: 4944-4959.

- [20] Zhang Q, Han C (2007) Convergence of numerical solutions to stochastic age-structured population system with diffusion. *Applied Mathematics and Computation* 186: 1234-1242.
- [21] Zeeman ML (1995) Extinction in competitive Lotka-Volterra systems. *Proceedings of the American Mathematical Society* 123: 87-96.

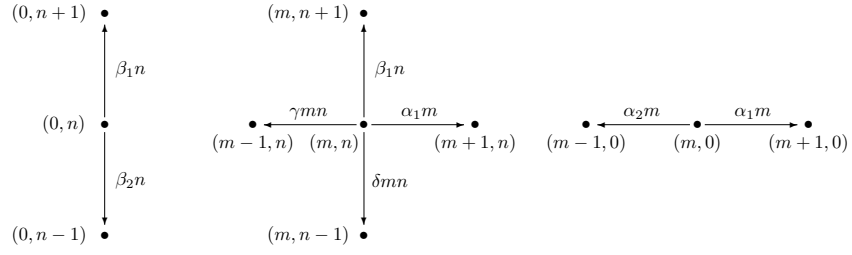


Figure 1: Transitions among states in the two-species competition process \mathcal{X}

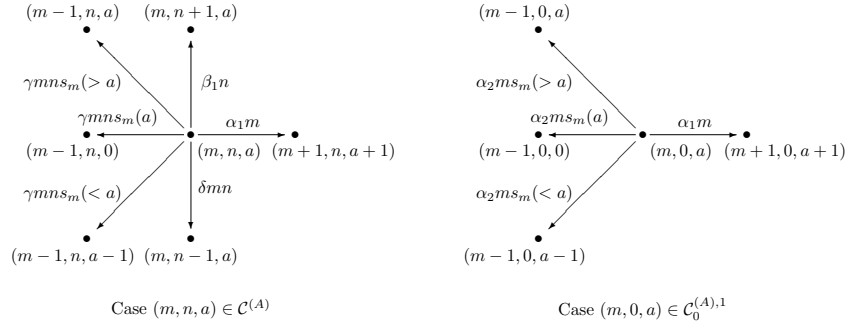


Figure 2: Transitions among augmented states

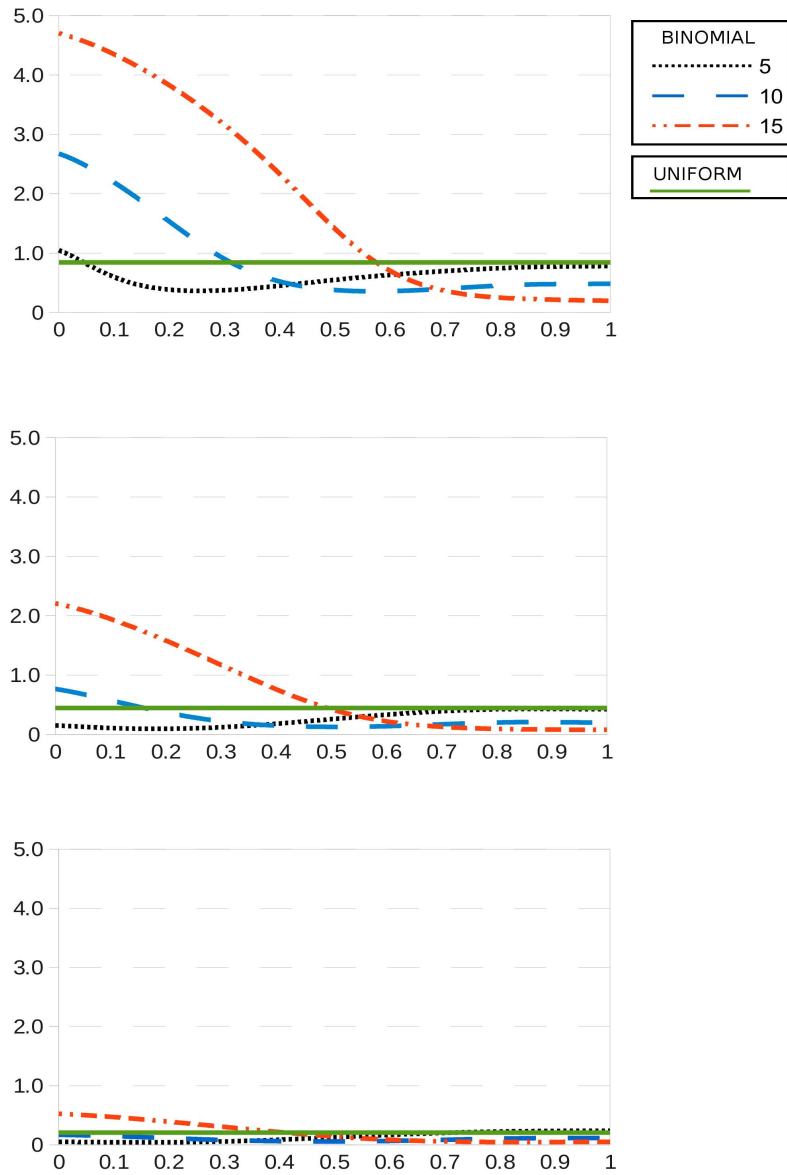


Figure 3: Expected residual lifetime versus the killing probability p_s for (from *top to bottom*) initial population sizes $(m, n) = (20, 10)$, $(20, 20)$ and $(20, 30)$, and initial ages $a \in \{5, 10, 15\}$. Killing strategies: $\mathbf{s}_{m'} \sim \text{Binomial}(m' - 1, p_s)$ and $\text{Uniform}\{1, 2, \dots, m'\}$, for $m' \in \mathbb{N}$.

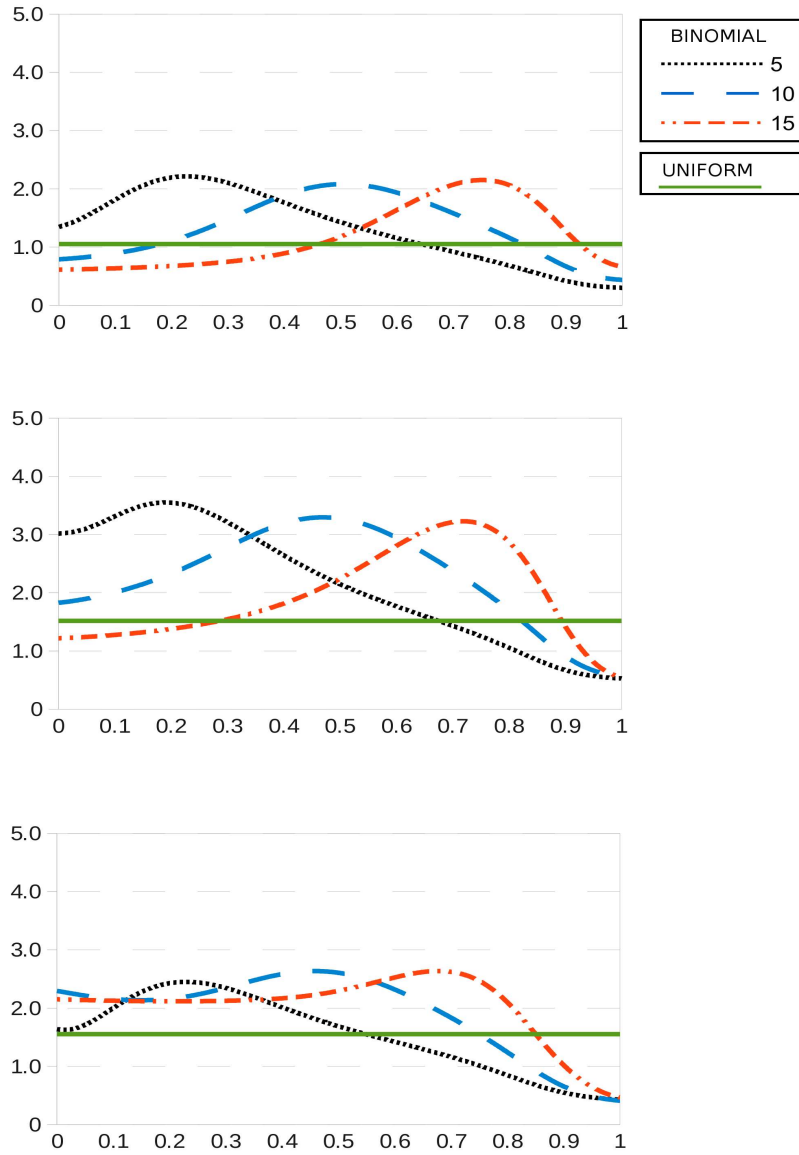


Figure 4: Variation coefficient of the residual lifetime versus the killing probability p_s for (from top to bottom) initial population sizes $(m, n) = (20, 10)$, $(20, 20)$ and $(20, 30)$, and initial ages $a \in \{5, 10, 15\}$. Killing strategies: $\mathbf{s}_{m'} \sim \text{Binomial}(m' - 1, p_s)$ and $\text{Uniform}\{1, 2, \dots, m'\}$, for $m' \in \mathbb{N}$.

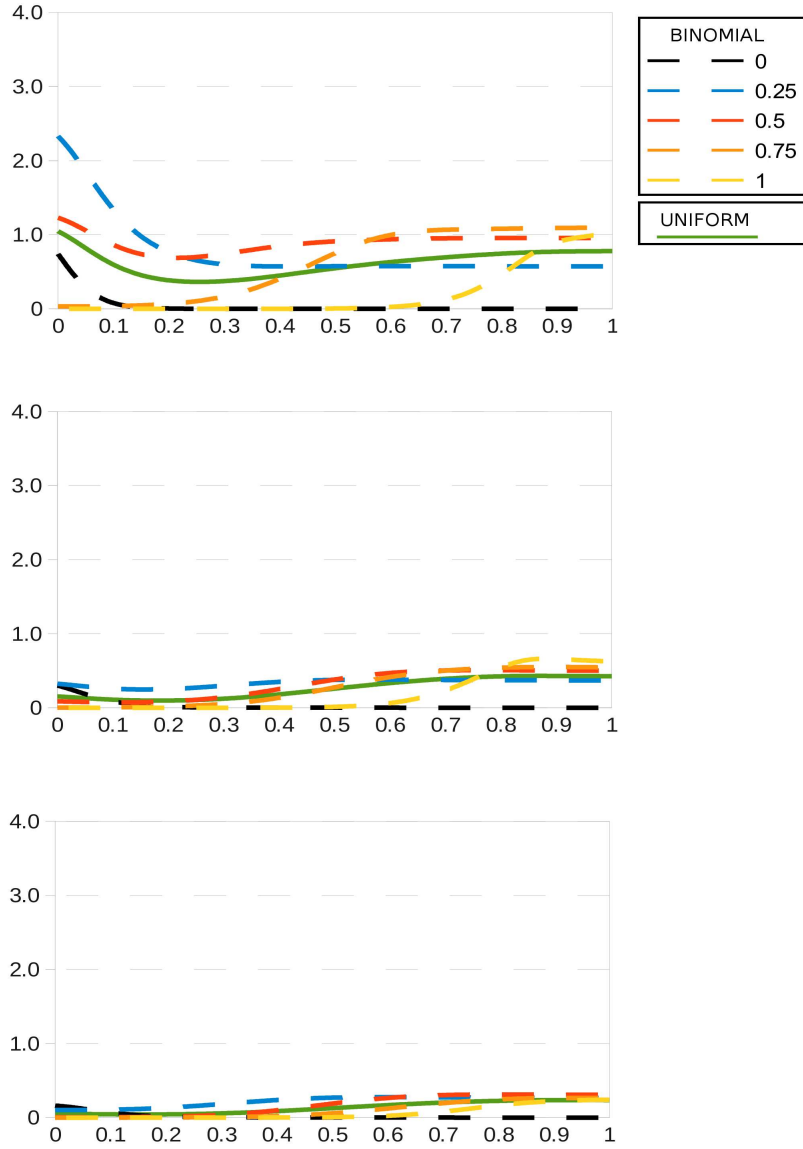


Figure 5: Expected number of descendants versus the killing probability p_s for (from *top* to *bottom*) initial populations sizes $(m, n) = (20, 10)$, $(20, 20)$ and $(20, 30)$, and initial age $a = 5$. Killing strategies: $\mathbf{s}_{m'} \sim \text{Binomial}(m' - 1, p_s)$, for $m' \in \mathbb{N}$; reproductive strategies: $\mathbf{r}_{m'} \sim \text{Binomial}(m' - 1, p_r)$ with $p_r \in \{0, 0.25, 0.5, 0.75, 1\}$, and $\text{Uniform}\{1, 2, \dots, m'\}$, for $m' \in \mathbb{N}$.

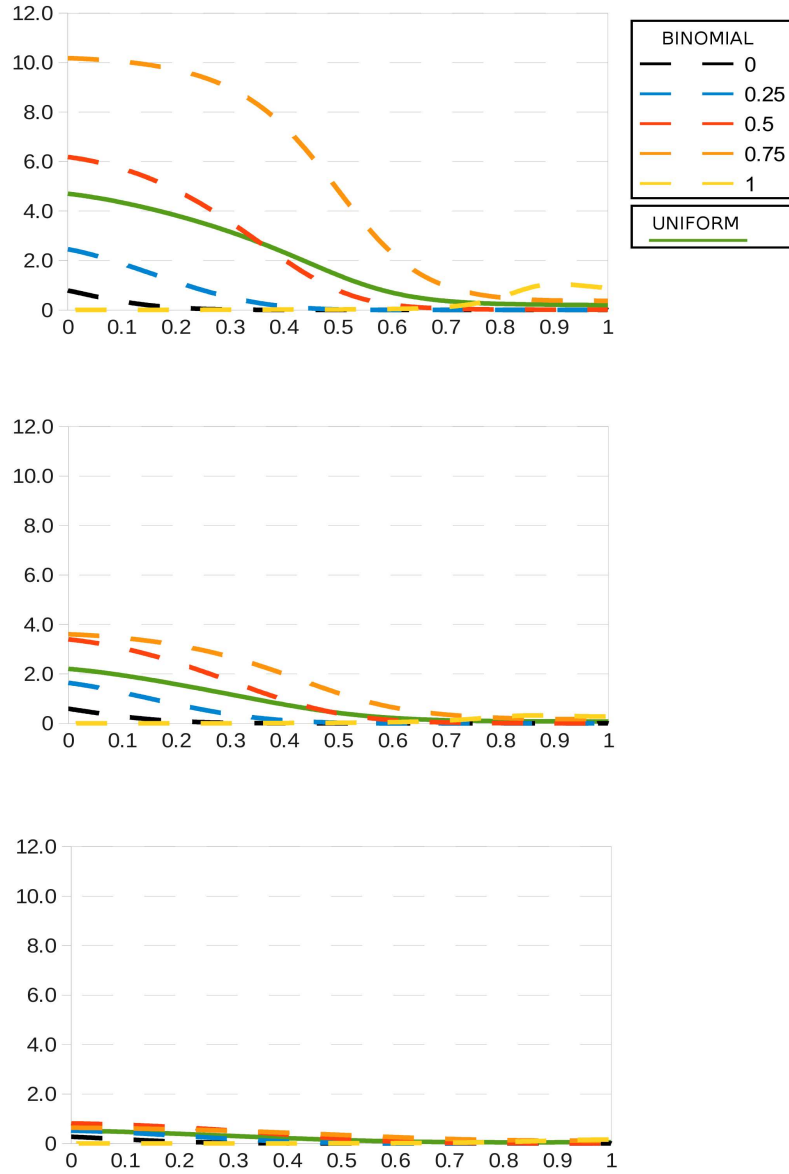


Figure 6: Expected number of descendants versus the killing probability p_s for (from *top* to *bottom*) initial populations sizes $(m, n) = (20, 10)$, $(20, 20)$ and $(20, 30)$, and initial age $a = 15$. Killing strategies: $\mathbf{s}_{m'} \sim \text{Binomial}(m' - 1, p_s)$, for $m' \in \mathbb{N}$; reproductive strategies: $\mathbf{r}_{m'} \sim \text{Binomial}(m' - 1, p_r)$ with $p_r \in \{0, 0.25, 0.5, 0.75, 1\}$, and $\text{Uniform}\{1, 2, \dots, m'\}$, for $m' \in \mathbb{N}$.

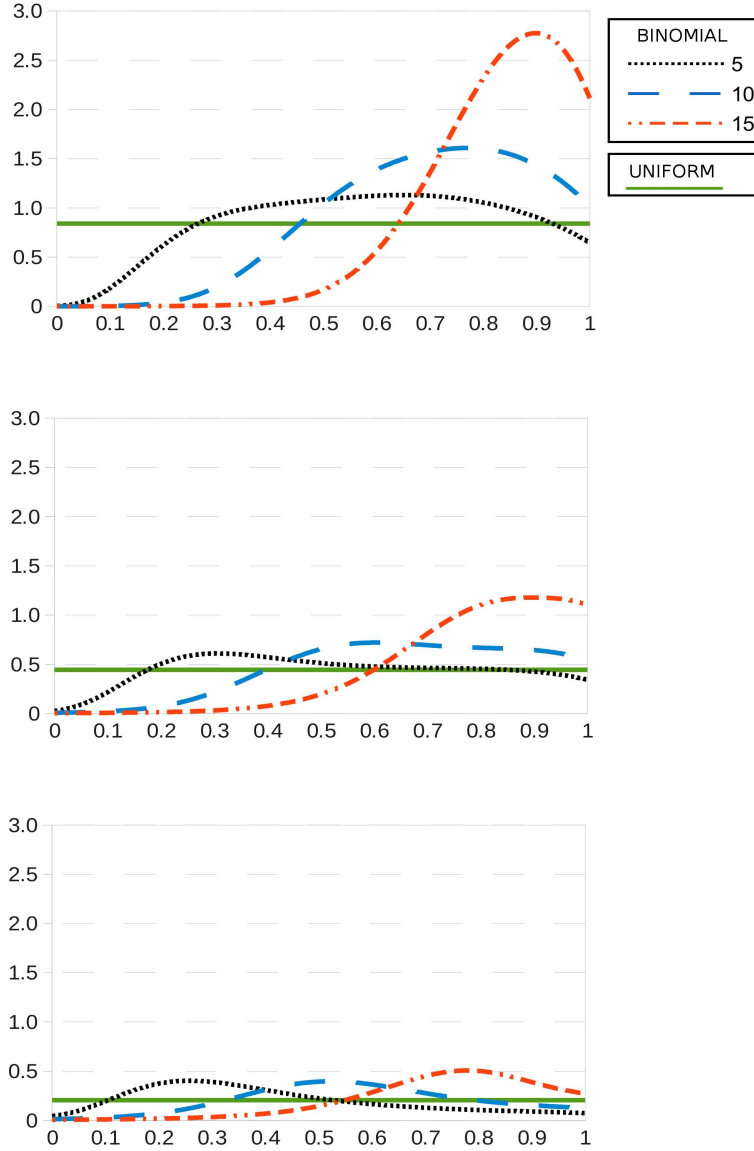


Figure 7: Expected number of descendants versus the reproductive probability p_r for (from *top to bottom*) initial populations sizes $(m, n) = (20, 10)$, $(20, 20)$ and $(20, 30)$, and initial ages $a \in \{5, 10, 15\}$. Killing strategies: $\mathbf{s}_{m'} \sim \text{Uniform}\{1, 2, \dots, m\}$; reproductive strategies: $\mathbf{r}_{m'} \sim \text{Binomial}(m' - 1, p_r)$ and $\text{Uniform}\{1, 2, \dots, m'\}$, for $m' \in \mathbb{N}$.

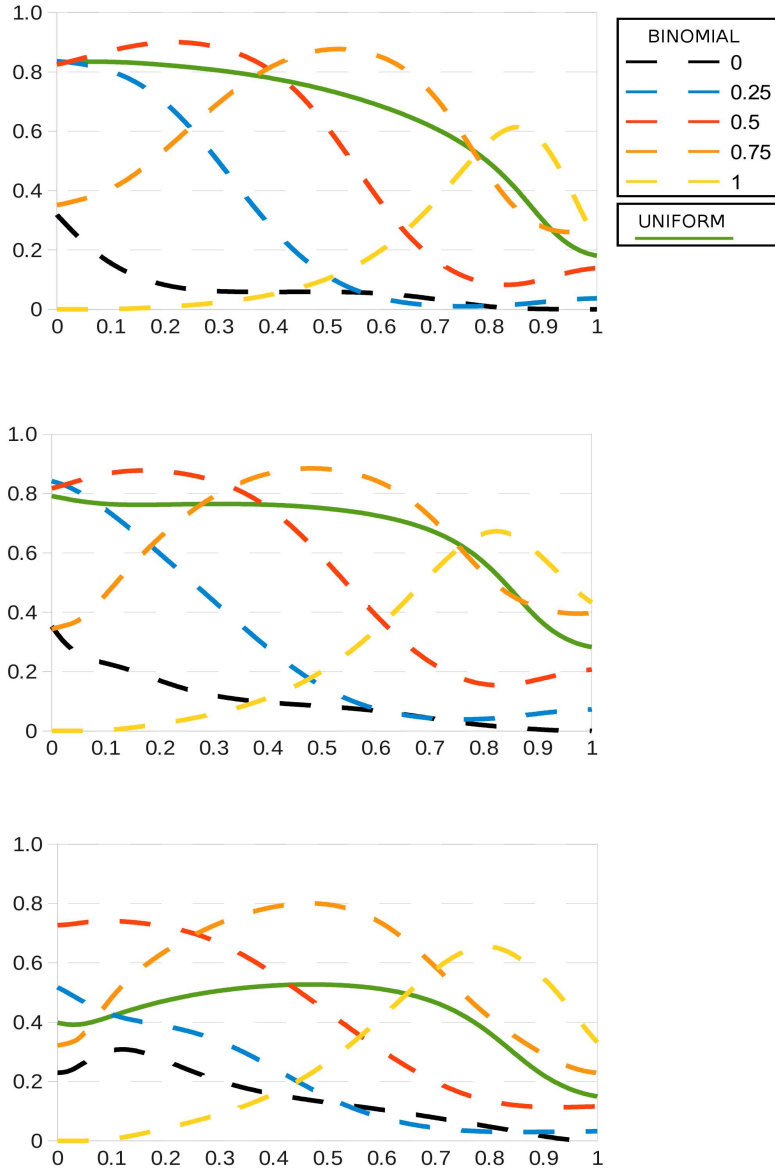


Figure 8: Coefficient of correlation versus the killing probability p_s for (from top to bottom) initial populations sizes $(m, n) = (20, 10)$, $(20, 20)$ and $(20, 30)$, and initial age $a = 5$. Killing strategies: $\mathbf{s}_{m'} \sim \text{Binomial}(m' - 1, p_s)$, for $m' \in \mathbb{N}$; reproductive strategies: $\mathbf{r}_{m'} \sim \text{Binomial}(m' - 1, p_r)$ with $p_r \in \{0, 0.25, 0.5, 0.75, 1\}$, and $\text{Uniform}\{1, 2, \dots, m'\}$, for $m' \in \mathbb{N}$.

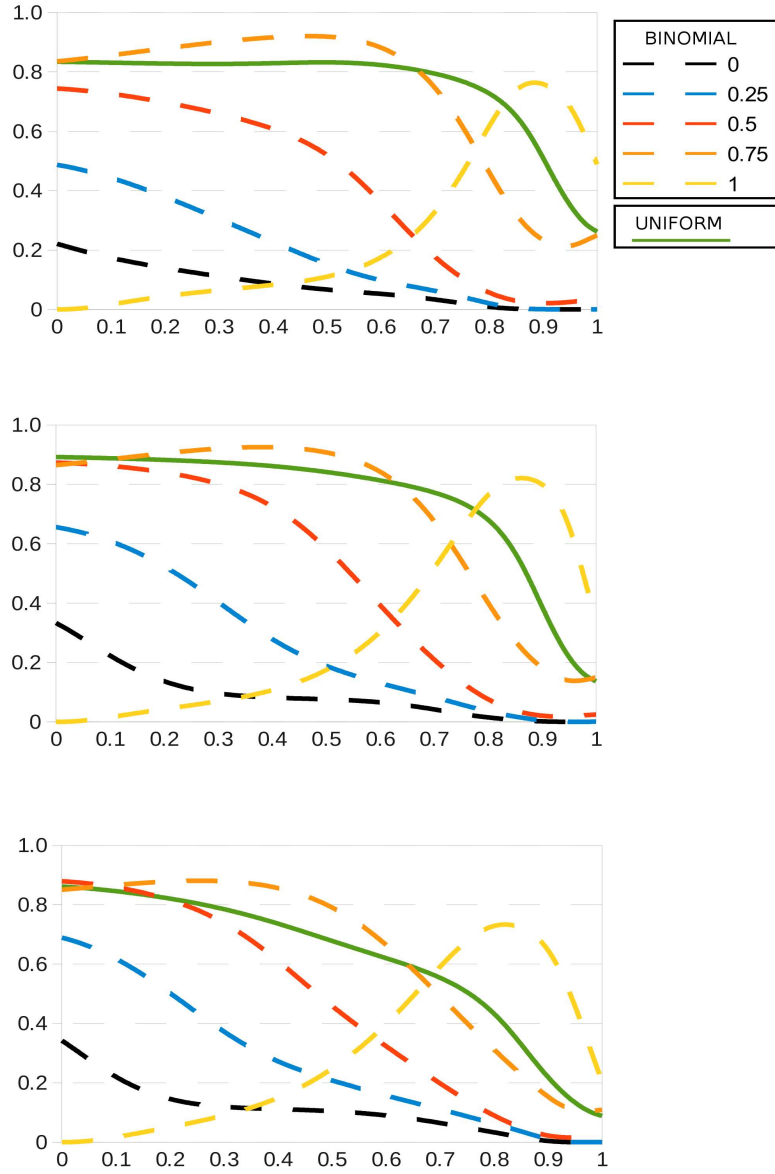


Figure 9: Coefficient of correlation versus the killing probability p_s for (from top to bottom) initial populations sizes $(m, n) = (20, 10)$, $(20, 20)$ and $(20, 30)$, and initial age $a = 15$. Killing strategies: $\mathbf{s}_{m'} \sim \text{Binomial}(m' - 1, p_s)$, for $m' \in \mathbb{N}$; reproductive strategies: $\mathbf{r}_{m'} \sim \text{Binomial}(m' - 1, p_r)$ with $p_r \in \{0, 0.25, 0.5, 0.75, 1\}$, and $\text{Uniform}\{1, 2, \dots, m'\}$, for $m' \in \mathbb{N}$.

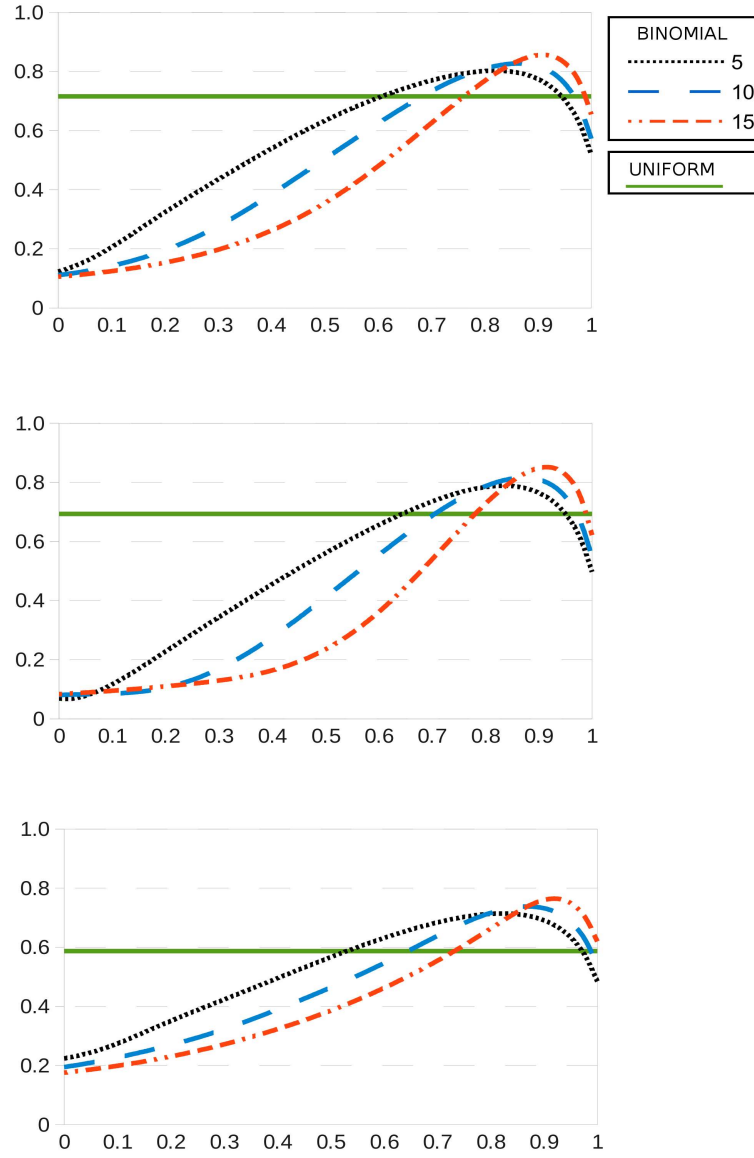


Figure 10: Coefficient of correlation versus the reproductive probability p_r for (from top to bottom) initial populations sizes $(m, n) = (20, 10)$, $(20, 20)$ and $(20, 30)$, and initial ages $a \in \{5, 10, 15\}$. Killing strategies: $\mathbf{s}_{m'} \sim Uniform\{1, 2, \dots, m'\}$, for $m' \in \mathbb{N}$; reproductive strategies: $\mathbf{r}_{m'} \sim Binomial(m' - 1, p_r)$ and $Uniform\{1, 2, \dots, m'\}$, for $m' \in \mathbb{N}$.