Journal of Statistical Mechanics: Theory and Experiment
An IOP and SISSA journal

PAPER: Biological modelling and information

Fixation in fluctuating populations

Deepak Bhat[1], **Jordi Piñero**[2,3] **and S Redner**[1]

[1] Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM, 87501, United States of America
[2] Complex Systems Lab, ICREA-Universitat Pompeu Fabra, Dr Aiguader 88, 08003 Barcelona, Spain
[3] Institut de Biologia Evolutiva, Psg. Barceloneta 37-49, 08003 Barcelona, Spain
E-mail: redner@buphy.bu.edu

Received 25 January 2019
Accepted for publication 24 April 2019
Published 13 June 2019

Online at stacks.iop.org/JSTAT/2019/063501
https://doi.org/10.1088/1742-5468/ab1ddd

Abstract. We investigate the dynamics of the voter model in which the population itself changes endogenously via the birth-death process. There are two species of voters, labeled A and B, and the population of each species can grow or shrink by the birth-death process at equal rates b. Individuals of opposite species also undergo voter model dynamics in which an AB pair can equiprobably become AA or BB with rate v—neutral evolution. In the limit $b/v \to \infty$, the distribution of consensus times varies as t^{-3} and the probability that the population size equals n at the moment of consensus varies as n^{-3}. As the birth/death rate b is increased, fixation occurs more more quickly; that is, population fluctuations promote consensus.

Keywords: population dynamics, stochastic processes, diffusion

J. Stat. Mech. (2019) 063501

© 2019 IOP Publishing Ltd and SISSA Medialab srl

1742-5468/19/063501+15$33.00

Contents

1. Introduction **2**

2. Uncoupled limit **3**

2.1. Two identical birth-death processes 4

2.1.1. Initial state: (A,B) = (1,1). 4

2.1.2. Initial state: (A,B) = (k, k). 5

3. The fluctuating voter model (FVM) **5**

4. Outlook **8**

Acknowledgments **9**

Appendix A. Generating function solution of the birth-death process **9**

Appendix B. Additional examples **10**

B.1. The initial state: (A,B) = (2,1) 10

B.2. Two distinct birth-death processes 11

B.3. k symmetric uncoupled species....13

References **14**

1. Introduction

A fundamental concept in evolutionary dynamics is that of *fixation*. In a population that consists of two (or more) species, demographic fluctuations or competitive effects can lead to a long-time state in which only one species remains, or fixates [1–5]. This fixation process has been extensively investigated in situations where the dynamics is defined to keep the total population constant. Indeed, in many evolutionary dynamics experiments on controllable systems, such as bacterial colonies, a typical protocol is to cull the population at fixed time intervals so that the population is the same at each of these resetting events [6]. However, in real bacterial colonies, the number of organisms changes with time. A pertinent example is when each species undergoes birth-death dynamics with equal birth and death rates for each species so that the average population is fixed but fluctuates endogenously.

We introduce the *fluctuating voter model* (FVM) to understand fixation in such a population. Here, two distinct species of voters can change their opinion state by voter-model dynamics [7–9] *and* the populations can grow or shrink by birth and death [9, 10] (figure 1). Our perspective is complementary to the modeling of biological populations in randomly switching environments [11–13]. The two species are equivalent in all respects except their identity. In a voter model update, which occurs at rate v, an AB pair transforms equiprobably to either AA or BB; that is, the evolution is neutral. We investigate the perfectly mixed limit, in which any pair of opposite-opinion voters is equally likely to interact. The voter model update is repeated *ad infinitum* or until

J. Stat. Mech. (2019) 063501

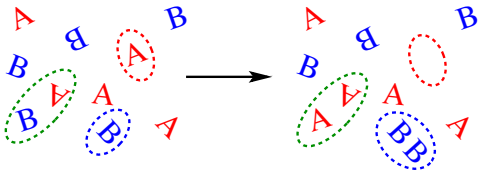

Figure 1. Cartoon of update events in the fluctuating voter model. An A dies with rate λ (red dashed oval), a B gives birth to another B also with rate λ (blue oval), and a circled AB pair changes to AA with rate v (green oval).

fixation (consensus) is reached, where only a single species remains. In addition, each individual can give birth to an offspring of the same type as the parent at rate λ, and each individual can die with rate μ.

By these mechanisms, the population and its composition change with time. Except for the pathological situation where the population grows exponentially in time (see, e.g. [14]), consensus is eventually reached. We assume that the birth and death rates equal a common value, $\lambda = \mu \equiv b$, so that the average population is fixed, but population fluctuations grow with time. Our main results are: (a) For $v/b \to 0$, fixation necessarily occurs and the distribution of fixation times $F(t)$ scales as t^{-3}; at fixation, the probability Q_n that the population size equals n scales as n^{-3}. (b) Population fluctuations promote fixation; the fixation time is a decreasing function of the birth/death rate b. (c) For arbitrary b and v, the fixation time distribution $F(t) \sim t^{-1-\beta}$, with β a function of b and v.

In the next section, we first treat the limit of $v/b \to 0$, where the system reduces to two uncoupled birth-death processes. Although the dynamics of a single birth-death process is very well understood, the properties of multiple birth-death processes appears unexplored, and we determine many of its basic properties analytically (see also the appendices). In section 3, we then outline our main results for the FVM.

2. Uncoupled limit

In the limit $v/b \to 0$, voter model updates do not occur and the birth-death processes for the two species decouple. We may therefore apply well-known results for the birth-death process to infer the extinction dynamics. For the single-particle initial condition, with the birth and death rates set to a common value b, the probability that there are n particles at time t is (see also appendix A) [9, 10]

$$P_n(t) = \frac{(bt)^{n-1}}{(1+bt)^{n+1}} \qquad\qquad P_0(t) = \frac{bt}{1+bt}, \tag{1}$$

from which the average population is $\langle n(t)\rangle = 1$, while the variance $\sigma^2 \equiv \langle n(t)^2\rangle - \langle n(t)\rangle^2 = 2bt$. Thus even though $\langle n(t)\rangle = 1$, there are huge population fluctuations between different realizations of the birth-death process.

Although the average population is fixed, its ultimate fate is extinction. From the second of equation (1), the survival probability $S_1(t)$, namely, the probability that a single birth-death process does not go extinct by time t is

J. Stat. Mech. (2019) 063501

$$S_1(t) = 1 - P_0(t) = \frac{1}{1+bt}, \tag{2a}$$

while the probability that extinction occurs at time t is

$$F_1(t) = -\frac{\mathrm{d}}{\mathrm{d}t} S_1(t) = \frac{b}{(1+bt)^2}. \tag{2b}$$

This birth-death process is *recurrent* (analogous to diffusion in one dimension [15, 16]), because the extinction probability $P_0 \to 1$ for $t \to \infty$, but the average time to reach extinction, $\langle t \rangle = \int_0^\infty \mathrm{d}t\, t\, F_1(t)$ is infinite.

2.1. Two identical birth-death processes

2.1.1. Initial state: (A,B) = (1,1). We study the dynamics of two uncoupled birth-death processes in which the initial state consists of one A and one B, and the common birth/death rates of each process are the same and equal to b. For extinction to not occur by time t, the number of particles in both of the two birth-death processes must remain non-zero. This probability is

$$S_2(t) = [S_1(t)]^2 = [1 - P_0(t)]^2 = \frac{1}{(1+bt)^2}. \tag{3a}$$

This quantity is also the probability that the extinction time is t or greater. Thus the probability that one of the two species goes extinct at time t is

$$F_2(t) = -\frac{\mathrm{d}}{\mathrm{d}t}[S_2(t)] = \frac{2b}{(1+bt)^3}. \tag{3b}$$

Because the exponent of this time dependence is less than -2, the average extinction time is finite:

$$\langle t \rangle = \int_0^\infty \mathrm{d}t\, t\, F_2(t) = \int_0^\infty \mathrm{d}t\, S_2(t) = \frac{1}{b}. \tag{4}$$

In contrast to a single birth-death process, the *smallest* extinction time among two independent birth-death processes is finite. A related dichotomy occurs in one-dimensional diffusion [16]: the average time for a single diffusing particle that starts at x to reach $x = 0$ is infinite, but for three particles that start at x, the smallest time for one of them to reach $x = 0$ is finite. Even though the average extinction time for two birth-death processes is finite, the mean-square time extinction time is divergent. Thus in a finite number of realizations of two independent birth-death processes, there will be huge sample-to-sample fluctuations in the time when the first species goes extinct.

At extinction, a natural characteristic is the average number of particles $\langle n \rangle$ of the surviving species. Since the birth-death process conserves the average particle number and the initial state consists of two particles, there must be two particles, on average, at any time, including the moment when one species goes extinct. We may also determine Q_n, the probability distribution for n. At time t, the probability that the number of particles in either species equals n is given by $P_n(t)$ in equation (1). To obtain Q_n, we convolve this distribution with the probability that the other birth-death process goes

J. Stat. Mech. (2019) 063501

extinct at time t, namely $F_1(t)$ in equation (2b). Thus the probability that the surviving population consists of n particles when the first species goes extinct is

$$Q_n = 2\int_0^\infty \mathrm{d}t\, F_1(t)P_n(t) = 2\int_0^\infty \mathrm{d}t\, \frac{b\,(bt)^{n-1}}{(1+bt)^{n+3}} = \frac{4\Gamma(n)}{\Gamma(n+3)} \simeq \frac{4}{n^3}. \tag{5}$$

The prefactor 2 accounts for the fact that either of the 2 species could go extinct first. Fortuitously, this expression for Q_n is identical to the degree distribution in linear preferential attachment networks [17]. We do not have any explanation for this remarkable coincidence. It is also straightforward to verify that when one species goes extinct the number of particles of the remaining species is $\langle n\rangle = \sum_{n\geqslant 1} nQ_n = 2$.

2.1.2. Initial state: $(A,B) = (k,k)$. We now briefly study the initial state with $k > 1$ particles of each species in the initial state. The expression for $P_n(t)$ for $n > 0$ becomes more unwieldy as k increases, and we only investigate the extinction dynamics. The probability that a single birth-death process with k particles in the initial state goes extinct at time t is $P_0(t) = [bt/(1+bt)]^k$ (see appendix A). From this expression, the probability that this birth-death process survives until time t is $S^{(k)}(t) = 1 - P_0$. The probability that two independent birth-death processes with the (k,k) initial condition survive until time t is $\left[S^{(k)}(t)\right]^2$. Consequently, the average time at which one of the two species first goes extinct is

$$\begin{aligned}\langle t\rangle &= \int_0^\infty \mathrm{d}t\,\left[S^{(k)}(t)\right]^2 = \int_0^\infty \mathrm{d}t\,\left[\frac{(1+bt)^k - (bt)^k}{(1+bt)^k}\right]^2 \\ &= \frac{2k}{b}\left[H_{2k} - H_k\right] \simeq \frac{2\,k\ln 2}{b},\end{aligned} \tag{6}$$

where H_n is the nth harmonic number, $H_n = \sum_{1\leqslant k\leqslant n}\frac{1}{k}$. The integral was performed using Mathematica [18], but an important preliminary step to get a simple result is to make the substitution $y = 1/bt$ in the integrand.

3. The fluctuating voter model (FVM)

We now investigate the dynamics of the FVM when the voting rate v and the birth/death rate b are both nonzero. Let N_A and N_B denote the respective number of voters of type A and B in a population of $N = N_A + N_B$ individuals, and let $x = N_A/N$ and $1 - x = N_B/N$ be the fraction of voters in each state. When the system is perfectly mixed, the total rate for an event to occur (either voting or birth/death) for $N \gg 1$ is $R = 2vNx(1-x) + 2bN$. We take the voting rate $v = 1$ henceforth and study the dynamics as a function of the birth/death rate b. With probability $2Nx(1-x)/R$ a voting event occurs in which an AB pair changes equiprobably to AA or BB. With the complementary probability $2bN/R$, an individual either gives birth or dies (figure 2). After each update, the time is incremented by an exponential random variable with mean value $1/R$. These updates are repeated until consensus is reached. The above defines the event-driven algorithm [19] for the time evolution.

J. Stat. Mech. (2019) 063501

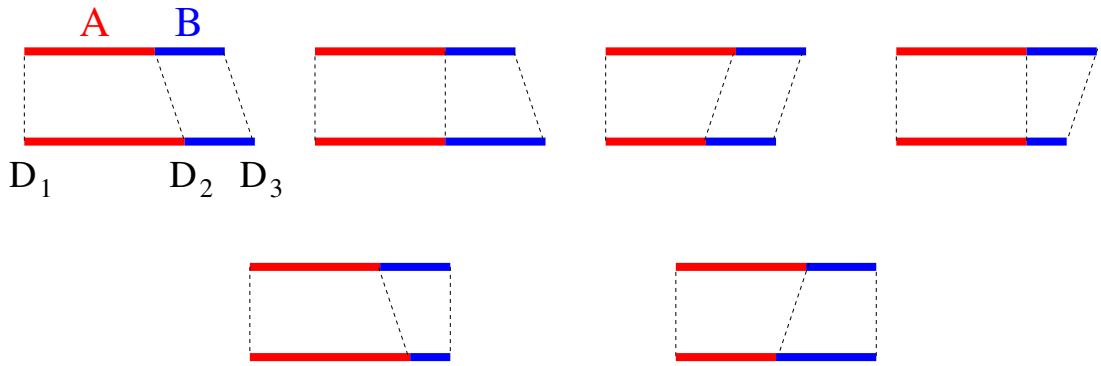

Figure 2. Representation of the FVM as an interval of length $N_A + N_B$. Top row: changes due to birth of an A, birth of a B, death of an A, and death of a B, respectively. Bottom row: changes due to the voting events AB $\to$ AA and AB $\to$ BB, respectively. The diffusion coefficients of the effective interface particles are indicated.

To understand the dynamics of FVM, it is helpful to first map its dynamics onto that of the reunion of three diffusing particles on the line, and finally to exploit known results about this three-particle problem [16] to predict the survival time distribution exponent. We first represent the FVM as a line interval that consists of two subintervals of lengths N_A and N_B (figure 2). The events of birth, death, and voting lead to the changes in the interval lengths indicated in the figure. Whenever the boundary between A's and B's reaches either the left or right end of the interval, extinction of one species occurs. The left end of the interval is stationary, by construction, and thus has diffusion coefficient $D_1 = 0$. By examining figure 2, we deduce that the AB interface particle and the right edge of the interval have respective diffusion coefficients

$$D_2 = \frac{2Nx(1-x) + 2bNx}{R} \qquad D_3 = \frac{2bN}{R}. \tag{7}$$

This three-particle system, with particles located at (x_1, x_2, x_3), can be mapped onto the diffusion of a single particle at (x_1, x_2, x_3) in three dimensions with absorbing boundary conditions whenever $x_1 = x_2$ or $x_2 = x_3$. This corresponds to the middle particle of the three-particle system reaching either end of the interval. In turn, this effective single-particle system in three dimensions subject to the constraint that the walk dies whenever $x_1 = x_2$ or $x_2 = x_3$ is isomorphic to a single diffusing particle in a two-dimensional absorbing wedge of opening angle θ, with (see [16] for a detailed explanation of this geometric argument)

$$\theta = \cos^{-1}\left[\frac{D_2}{\sqrt{(D_1 + D_2)(D_2 + D_3)}}\right]. \tag{8a}$$

The survival probability for the middle particle, which is the same as the probability that extinction has not yet occurred is known to scale as $t^{-\beta}$, with $\beta = \pi/2\theta$ [16]. Figure 3(a) shows our simulation results for the time dependence of the survival probability, which indicates a power-law temporal decay with a non-universal exponent.

To determine the exponent β, we need to apply equation (8a) to the FVM. Here we need to account for the position (x) dependence of the diffusion coefficients in

J. Stat. Mech. (2019) 063501

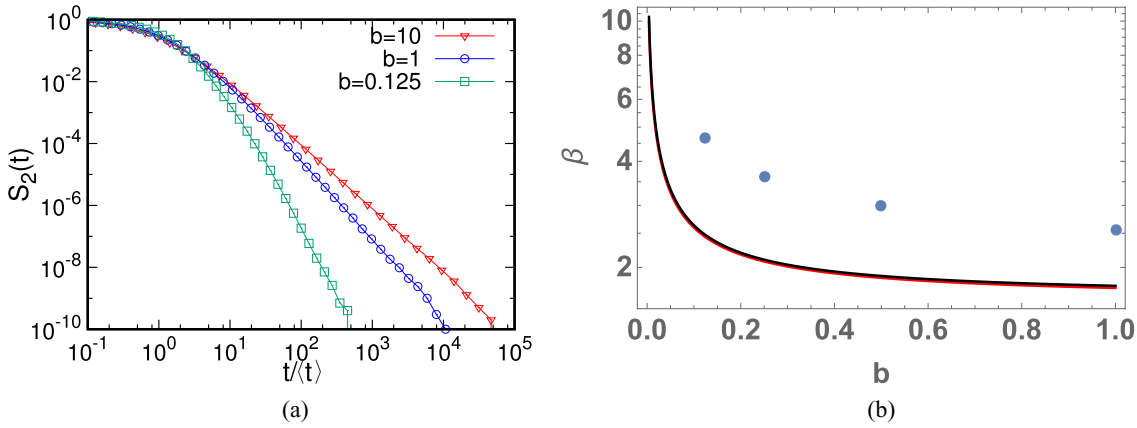

Figure 3. (a) Survival probability $S_2(t)$ versus $t/\langle t\rangle$ for representative b values. The data are based on 10^{10} realizations. (b) The survival probability exponent β versus birth rate b predicted by (8a) (black) and the more principled averaging procedure discussed in the text (red). The points are estimates for β from simulations.

equation (7). The simplest scheme is to merely replace the true diffusion coefficients in (7) with their values when the expressions $x(1-x)$ and x in (7) are averaged over the interval. For this prescription, we assume that the interface position is uniformly distributed over the interval, which gives $\langle x(1-x)\rangle = \frac{1}{6}$. In fact, the probability distribution of x is uniformly distributed over the interval for the mean-field voter model in the long-time limit [20]. With this ansatz, we obtain, after some simple algebra,

$$\beta = \pi \Big/ 2\cos^{-1}\left[\frac{1+3b}{\sqrt{1+12b+27b^2}}\right]. \tag{8b}$$

A more principled procedure would be to include the x-dependence of the diffusion coefficients in the expression for $\beta = \pi/\big[2\theta(x)\big]$ and then numerically average this expression uniformly over the interval. This procedure leads to a result that closely matches (8b) (figure 3(b)).

The main features of equation (8b) is that the exponent β monotonically increases as b decreases (and is slowly varying in b for $b \gtrsim \frac{1}{2}$). The values of the survival probability exponent β from equation (8b) as a function of b is shown in figure 3(b). Estimates of β from simulation data for various b values are also shown in this figure to give a sense of the accuracy of our analytical approach. It is not feasible to obtain reliable estimates of β from simulation for smaller b because the exponent becomes quite large. Conversely, for larger b, the exponent β from simulations is nearly constant.

There is also an important effect that is not accounted for in equation (8a)—the motions of the middle and right particles are correlated. When an A either gives birth or dies, the middle and right particles in figure 2 move in lockstep. This implies that the motion of the effective particle in the wedge is not isotropic. While we do not know how to account for these two effects rigorously—averaging over the interval and the correlation in the effective particle motions—our heuristic approach gives the qualitatively correct dependence of the survival probability exponent β on b. We can also get a sense of the role of correlations in the effective particle motions on the exponent β by considering the $b \to \infty$ limit. Here, voter model updates do not occur, so there is

J. Stat. Mech. (2019) 063501

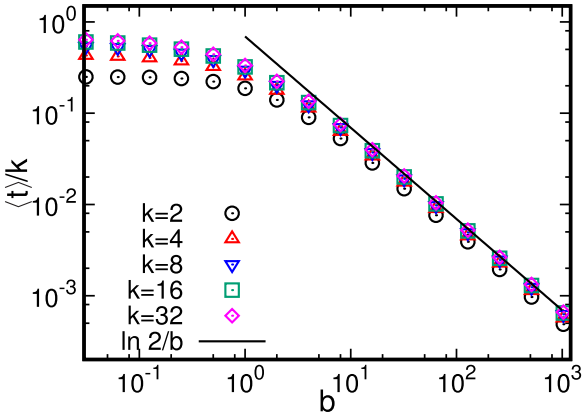

Figure 4. Average fixation time $\langle t \rangle$ divided by k versus b for various initial populations k. The data are based on 10^6 realizations for each point. The straight line is the prediction of equation (6).

no position dependence in the particle diffusion coefficients. Now equation (8*b*) should be directly applicable and it gives $\beta = \pi/\left[2\cos^{-1}(1/\sqrt{3})\right] \approx 1.644$, whereas, the exact exponent from equation (3*a*) is 2.

Finally, we investigate the dependence of the fixation time on the birth rate (figure 4). The primary observation from these simulations is that the fixation time is a monotonically decreasing function of the birth rate b. That is, population fluctuations promote fixation. In a related vein, the more stable (less volatile) species is more likely to fixate for non-zero voting rate.

4. Outlook

We investigated basic properties of fixation in a fluctuating population. The population consists of two distinct species, A and B, that are identical in all dynamical respects, except for their label. The population of each species grows and shrinks by the classic birth-death process and, in addition, AB pairs can transform to AA or BB by voter model dynamics.

In the limit of voting rate $v = 0$, the system reduces to two independent birth-death processes, for which many interesting results can be derived analytically. Although a single birth-death process has an infinite average extinction time, the fixation time for two independent birth-death processes (the time when one species first goes extinct) is finite. The distribution of fixation times asymptotically decays as t^{-3}, while the distribution of the number n of surviving species decays as n^{-3}. These properties are robust with respect to the initial condition and also to different birth/death rates for each species. When the voting rate is non-zero, a basic outcome is that the fixation time is reduced by birth-death fluctuations. That is, population volatility leads to quicker extinction.

There are many directions for future research. We only investigated situations where the birth and death rates for each species are equal, and extending to unequal birth and

J. Stat. Mech. (2019) 063501

death rates may reveal new phenomena. It would also be interesting to include spatial degrees of freedom into the dynamics, as this aspect naturally arises in any bacterial colony, and fixation phenomena have been extensively investigated in growing bacterial colonies (see [21] for a review).

Acknowledgments

We thank Jacopo Grilli for helpful discussions. DB and SR gratefully acknowledge NSF financial support from grant DMR-1608211. JP acknowledges support from 'María de Maeztú' fellowship MDM-2014-0370-17-2, from Botin Foundation, by Banco Santander through its Santander Universities Global Division and by FIS2015-67616-P.

Appendix A. Generating function solution of the birth-death process

We outline some basic facts about the classic birth-death process, in which a population of independent organisms grows or shrinks because each organism gives birth at rate λ or dies with rate μ. Let $P_n(t)$ denote the probability that there are n organisms at time t. This probability changes with time by according to

$$\dot{P}_n = \lambda\big[(n-1)P_{n-1} - nP_n\big] + \mu\big[(n+1)P_{n+1} - nP_n\big]. \tag{A.1a}$$

The relevant case is that of equal birth and death rates, so that the average population is stationary. In this limit, the master equation reduces to

$$\dot{P}_n = (n-1)P_{n-1} - 2nP_n + (n+1)P_{n+1}, \tag{A.1b}$$

where we set $\lambda = \mu = 1$.

A convenient way to solve these equations is by the generating function method [9, 22]. We define the generating function $g(z,t) = \sum_{n\geqslant 0} P_n z^n$, multiply equation (A.1$a$) by z^n, and sum over all n. After some standard manipulations that involve converting terms like $\sum_n nP_n z^n$ into a derivative with respect to z, the generating function satisfies $g_t = (1-z)^2 g_z$, where the subscripts denote partial differentiation. We convert this to the elementary wave equation $g_t = g_y$ by defining the variable $dy = dz/(1-z)^2$, from which we obtain $y = 1/(1-z)$, or $z = 1 - y^{-1}$. The solution to the wave equation is $g(y,t) = F(y+t)$, where F is an arbitrary function that is fixed by the initial condition.

For the single particle initial condition, $P_n(t=0) = \delta_{n,1}$. Then $g(z,t=0) = z$. Because the natural variables for the generating function are (y,t) instead of (z,t), we re-express the initial generating as $g(y,t=0) = z = F(y) = 1 - y^{-1}$. Since the generating function depends on the variable combination $y+t$, we have, for $t>0$, $g(y,t) = 1 - (t+y)^{-1}$. Finally, we re-express the generating function in terms of (z,t) to give

$$g(z,t) = 1 - \frac{1}{t + \frac{1}{1-z}}. \tag{A.2a}$$

We now write this last expression in a Taylor series in z to extract P_n and P_0 given in equation (1). To incorporate an arbitrary birth rate b, as in (1), we merely make the substitution $t \to bt$.

J. Stat. Mech. (2019) 063501

The above derivation can be straightforwardly extended to the initial condition of k particles. Now the initial generating function is $g(z,t=0)=z^k$, and following the steps of the previous paragraph, the generating function is

$$g(z,t)=\left(1-\frac{1}{t+\frac{1}{1-z}}\right)^k. \tag{A.2b}$$

For the two-particle initial condition ($k=2$), the Taylor series expansion of the generating function give P_n and P_0 written in equation (B.1). For larger k, the Taylor series expansion of $g(z,t)$ becomes progressively more unwieldy. However, the form of P_0 for general k is simple: $P_0(t)=\big[t/(1+t)\big]^k\to\big[bt/(1+bt)\big]^k$.

Appendix B. Additional examples

The presentation in section 2.1 can be readily extended to other initial conditions and to more than two uncoupled birth-death processes. Because these examples have illustrative value, we discuss these two cases below.

B.1. The initial state: (A,B) = (2,1)

We first generalize the derivations in section 2.1 to unequal initial numbers of particles of each species. For specificity, we treat the initial state of of 2 A's and 1 B; it is straightforward to extend our approach to more general initial conditions. For a single birth-death process starting with two particles, the distribution $P_n(t)$ now is (from the Taylor series expansion of equation (A.2a))

$$P_n(t)=\frac{2(bt)^n+(n-1)(bt)^{n-2}}{(1+bt)^{n+2}} \qquad P_0(t)=\left(\frac{bt}{1+bt}\right)^2. \tag{B.1}$$

This distribution satisfies $\sum_{n\geqslant 0}P_n=1$ and conservation of the average particle number, $\langle n(t)\rangle=\sum_{n\geqslant 1}nP_n=2$. From this expression for P_0, the probability that the A's survive until time t, for the $(2,1)$ initial condition, is

$$S^{(\mathrm{A})}(t)=1-P_0=\frac{1+2bt}{(1+bt)^2}, \tag{B.2a}$$

from which the probability that A's go extinct at time t is

$$F^{(\mathrm{A})}(t)=-\frac{\mathrm{d}}{\mathrm{d}t}S^{(\mathrm{A})}(t)=\frac{2b^2t}{(1+bt)^3}, \tag{B.2b}$$

while $S^{(\mathrm{B})}$ and $F^{(\mathrm{B})}$ are again given by (2).

The probability that both birth-death processes do not go extinct by time t is $S_2(t)=S^{(\mathrm{A})}(t)\,S^{(\mathrm{B})}(t)$, while the probability that extinction occurs at time t is (without regard to which species goes extinct)

$$F_2(t)=-\frac{\mathrm{d}}{\mathrm{d}t}S_2(t)=\frac{b(1+4bt)}{(1+bt)^4}. \tag{B.3}$$

J. Stat. Mech. (2019) 063501

In analogy with (4), the average time for the first extinction to occur, irrespective of which species goes extinct is now

$$\langle t\rangle = \int_0^\infty \mathrm{d}t\, t\, F_2(t) = \int_0^\infty \mathrm{d}t\, S_2(t) = \frac{3}{2b}. \tag{B.4}$$

The extinction time is longer than in equation (4) because the population initially is 'further' from extinction—three particles rather than two. It is also natural to ask which of the two species goes extinct first. The probability $\mathcal{E}^{(\mathrm{A})}$ that species A goes extinct first is

$$\mathcal{E}^{(\mathrm{A})} = \int_0^\infty \mathrm{d}t\, F^{(\mathrm{A})}(t)\, S^{(\mathrm{B})}(t) = \int_0^\infty \mathrm{d}t\, \frac{2t}{(1+t)^4} = \frac{1}{3}. \tag{B.5}$$

In this integral, the factor $F^{(\mathrm{A})}$ ensures that A's go extinct at time t while the factor $S^{(\mathrm{B})}$ ensures that the B's are not extinct at this time. Similarly, the probability $\mathcal{E}^{(\mathrm{B})}$ that species B first goes extinct equals $\frac{2}{3}$.

Finally, the probability that the population consists of n particles of type A at the moment of B extinction is

$$Q_n^{(\mathrm{A})} = \int_0^\infty \mathrm{d}t\, F^{(\mathrm{B})}(t)\, P_n^{(\mathrm{A})}(t) = \int_0^\infty \mathrm{d}t\, b\, \frac{2(bt)^n + (n-1)(bt)^{n-2}}{(1+bt)^{n+4}}$$
$$= \begin{cases} \frac{4(n+6)\Gamma(n)}{\Gamma(n+4)} & n > 1 \\ \frac{1}{6} & n = 1. \end{cases} \tag{B.6a}$$

Similarly, the probability that the population consists of n particles of type B at the moment of A extinction is

$$Q_n^{(\mathrm{B})} = \int_0^\infty \mathrm{d}t\, F^{(\mathrm{A})}(t)\, P_n^{(\mathrm{B})}(t) = \int_0^\infty \mathrm{d}t\, b\, \frac{2(bt)^n}{(1+bt)^{n+4}} = \frac{4\Gamma(n+1)}{\Gamma(n+4)}. \tag{B.6b}$$

Both of the distributions in equation (B.6) asymptotically scale as $4n^{-3}$ for $n \to \infty$.

The distributions Q_n satisfy the basic sum rules:

$$\sum_{n\geqslant 1} Q_n^{(\mathrm{A})} = \frac{2}{3} \qquad \sum_{n\geqslant 1} Q_n^{(\mathrm{B})} = \frac{1}{3}; \qquad \sum_{n\geqslant 1} nQ_n^{(\mathrm{A})} = 2 \qquad \sum_{n\geqslant 1} nQ_n^{(\mathrm{B})} = 1. \tag{B.7}$$

The first two relations state that the probability that A's are the surviving species equals $\frac{2}{3}$, while B's are the surviving species with probability $\frac{1}{3}$. The next two relations state that the average number of A's, conditioned on B's going extinct, equals 2, while the average number of B's, conditioned on A's going extinct, equals 1. Thus the average number of surviving particles at the moment of extinction, independent of their identity, equals 3.

B.2. Two distinct birth-death processes

Suppose that the common birth/death rates for the two species are different; we denote these rates as a and b for species A and B, respectively. The probability that both birth-death processes do not go extinct by time t is (compare with equation (2a))

J. Stat. Mech. (2019) 063501

$$S_2(t) = \frac{1}{(1+at)}\frac{1}{(1+bt)}, \tag{B.8}$$

which we again term the survival probability. The probability that one of the species goes extinct at time t is (compare with equation (2*b*))

$$F_2(t) = -\frac{dS_2(t)}{\mathrm{d}t} = \frac{a}{(1+at)^2(1+bt)} + \frac{b}{(1+bt)^2(1+at)} = F_1^{(\mathrm{A})}(t)\, S_1^{(\mathrm{B})}(t) + F_1^{(\mathrm{B})}(t)\, S_1^{(\mathrm{A})}(t), \tag{B.9}$$

where the superscripts refer to the species type. The first term on the right-hand side is the probability that species A goes extinct at time t while species B survives, and vice versa for the second term. The average extinction time, independent of which species goes extinct, is

$$\langle t\rangle = \int_0^\infty \mathrm{d}t\, t\, F_2(t) = \frac{\ln(b/a)}{b-a}. \tag{B.10}$$

For a, b both approaching the common value b, the above result reduces to $\langle t\rangle = 1/b$, given in equation (4).

It is natural to ask which species is more likely to go extinct—the more volatile or the more stable species. The probability $E^{(\mathrm{A})}$ that species A goes extinct is

$$E^{(\mathrm{A})} = \int_0^\infty \mathrm{d}t\, F_1^{(\mathrm{A})}(t)\, S_1^{(\mathrm{B})}(t) = \int_0^\infty \mathrm{d}t\, \frac{a}{(1+at)^2}\frac{1}{(1+bt)} = \frac{a\big[a-b+b\ln(b/a)\big]}{(a-b)^2}. \tag{B.11}$$

The factor $F_1^{(\mathrm{A})}$ ensures that it is species A that goes extinct, while the factor $S_1^{(\mathrm{B})}$ ensures that B's still survive when A goes extinct. Integrating this product over all time gives the total probability that species A goes extinct. From (B.11), it is likelier that the more volatile species goes extinct for the symmetric initial condition (figure B1(a)).

We also determine the *conditional* extinction times, namely, the average time for a specified species to go extinct. The average time for species A to go extinct is given by

$$\langle t^{(\mathrm{A})}\rangle = \int_0^\infty \mathrm{d}t\, t\, F_1^{(\mathrm{A})}(t)\, S_1^{(\mathrm{B})}(t) \Big/ \int_0^\infty \mathrm{d}t\, F_1^{(\mathrm{A})}(t)\, S_1^{(\mathrm{B})}(t) = \frac{b-a+a\ln(b/a)}{a\big[b-a+b\ln(b/a)\big]}. \tag{B.12}$$

The average time $\langle t^{(\mathrm{B})}\rangle$ for species B to go extinct is just the above expression with a and b interchanged. Figure B1(b) shows these extinction times for $b = 1$ and varying a; we see that increased volatility decreases the extinction time.

At the instant when species B goes extinct, Mathematica [18] gives the distribution of the number of species A that remain as (compare with equation (5))

$$\begin{aligned} Q_n^{(\mathrm{A})} &= \int_0^\infty \mathrm{d}t\ \ F_1^{(\mathrm{B})}(t)\, P_n^{(\mathrm{A})}(t) = \int_0^\infty \mathrm{d}t\ \frac{b}{(1+bt)^2}\,\frac{(at)^{n-1}}{(1+at)^{n+1}} \\ &= \frac{\alpha}{(\alpha-1)^3}\left\{\left[\frac{\alpha}{n} + \frac{(n^2+1)}{n(n-1)} - \frac{\big[2\alpha+(n-1)\big]\,{}_2F_1\,(1,1;3-n;\alpha)}{n-2}\right]\right. \\ &\qquad \left. -\frac{\pi\alpha^{n-1}}{(1-\alpha)^{n+2}}\big[2\alpha+1(n-1)\big]\csc(n\pi)\right\}, \end{aligned} \tag{B.13}$$

J. Stat. Mech. (2019) 063501

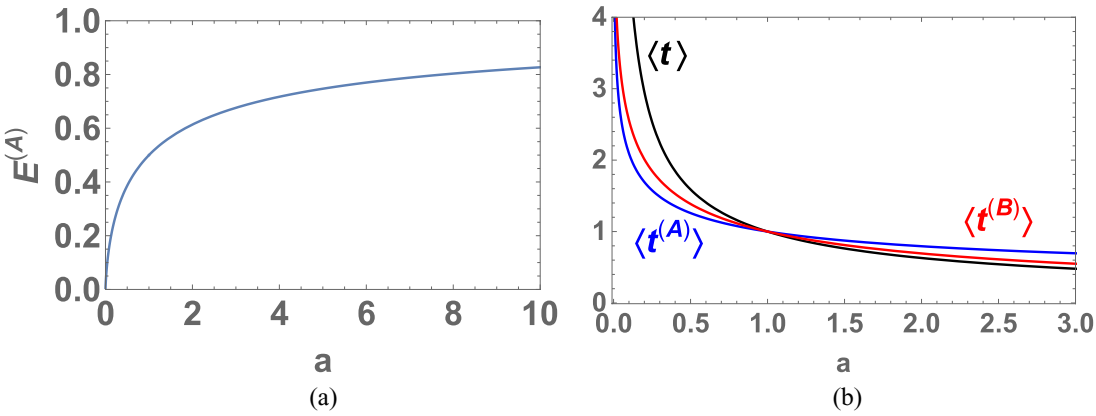

Figure B1. (a) The exit probability $E^{(\mathrm{A})}$ that species A goes extinct first as a function of its birth rate a. (b) Unconditional and conditional extinction times as a function of the birth rate a. In both panels, the birth/death rate of species B is fixed at $b = 1$ and the initial state contains of one particle of each species.

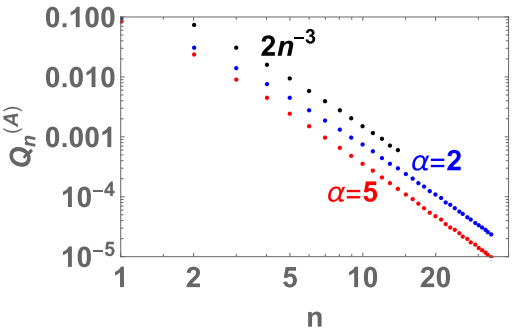

Figure B2. Numerical integration of $Q_n^{(\mathrm{A})}$ in equation (B.13) versus n on a double logarithmic scale for $n \leqslant 40$.

where $\alpha = a/b$. Unfortunately, this representation is pathological for all positive integer n: the hypergeometric function ${}_2F_1$ diverges for all $n \geqslant 3$, so that the first square bracket is diverges for all $n \geqslant 0$, but these divergences are all canceled by the term $\csc(n\pi)$. A numerical evaluation of this integral clearly shows that Q_n asymptotically scales as n^{-3} for all α (figure B2), with a coefficient that is a decreasing function of α.

B.3. *k* symmetric uncoupled species

Finally, we treat the case of k distinct species that all have common birth/death rates. We treat the initial condition of a single particle of each species. As a function of time, a series of partial extinctions occurs, in which the number of extant species decreases by 1 before the final extinction where only a single species remains. To determine the time for the first extinction, we use the fact that the probability that k independent birth-death processes do not go extinct before time t is $S_k(t) = [S_1(t)]^k$, with S_1 given by (2a). Thus $S_k(t)$ is the probability that the first extinction time is t or greater. The probability that this first extinction occurs at time t therefore is (compare with equation (2b))

J. Stat. Mech. (2019) 063501

$$F_k(t) = -\frac{dS_k(t)}{\mathrm{d}t} = k[S_1(t)]^{k-1}F_1(t) = \frac{kb}{(1+bt)^{(k+1)}}, \tag{B.14}$$

and the average time for the first extinction is

$$\langle t\rangle = \int_0^\infty \mathrm{d}t\, t\, F_k(t) = \int_0^\infty \mathrm{d}t\, S_k(t) = \frac{1}{(k-1)b}. \tag{B.15}$$

The number of particles of each species at the first extinction can be obtained by particle conservation. When there is 1 particle of each species in the initial state, these k initial particles will be equally distributed among the $k-1$ remaining species at the first extinction. Thus there will be $k/(k-1)$ particles of each species, on average, at the first extinction. At each subsequent extinction, the k initial particles will be equally distributed among the remaining species.

For the initial state that consists of k distinct species, with one particle of each species, we also calculate $Q_n^{(k)}$, the distribution of the number of particles in one of the $k-1$ remaining species at the first extinction event. The generalization of equation (5) is

$$\begin{aligned} Q_n^{(k)} &= \frac{k}{k-1}\int_0^\infty \mathrm{d}t\, F_{k-1}(t)P_n(t) = k\int_0^\infty \mathrm{d}t\, F_1(t)P_n(t)\big[S_1(t)\big]^{k-2} \\ &= \frac{k\Gamma(k+1)\Gamma(n)}{\Gamma(k+n+1)} \simeq k\Gamma(k+1)n^{-(k+1)}. \end{aligned} \tag{B.16}$$

The prefactor k accounts for the fact that any of the k initial species could go extinct first, while the factor $k-1$ in the denominator arises because we are counting only one of the $k-1$ remaining species. With these definitions, we recover the obvious sum rules, $\sum_{n\geqslant 1} Q_n^{(k)} = 1$ and $\sum_{n\geqslant 1} nQ_n^{(k)} = k/(k-1)$. In each subsequent extinction, the distribution of the number of particles in any one of the remaining species becomes gradually broader until $Q_n \sim n^{-3}$ when only a single species remains.

References

[1] Moran P A P 1962 *The Statistical Processes of Evolutionary Theory* (Oxford: Clarendon)
[2] Kimura M 1983 *The Neutral Theory of Molecular Evolution* (Cambridge: Cambridge University Press)
[3] Ewens D W 2004 *Mathematical Population Genetics* (Berlin: Springer)
[4] Nowak M A 2006 *Evolutionary Dynamics* (Cambridge, MA: Harvard University Press)
[5] Crow J F and Kimura M 2009 *An Introduction to Population Genetics Theory* (New Jersey: Blackburn Press)
[6] Good B H, McDonald M J, Barrick J E, Lenski R E and Desai M M 2017 *Nature* **551** 45
[7] Liggett T M 1999 *Stochastic Interacting Systems: Contact, Voter, and Exclusion Processes* (New York: Springer)
[8] Krapivsky P L 1992 *Phys. Rev.* A **45** 1067
[9] Krapivsky P L, Redner S and Ben-Naim E 2010 *A Kinetic View of Statistical Physics* (Cambridge: Cambridge University Press)
[10] Kendall D G 1949 *J. R. Stat. Soc. Series* B **11** 230
[11] Hufton P G, Lin Y T, Galla T and McKane A J 2016 *Phys. Rev.* E **93** 052119
[12] Hidalgo J, Suweis S and Maritan A 2017 *J. Theor. Biol.* **413** 1
[13] Wienand K, Frey E and Mobilia M 2017 *Phys. Rev. Lett.* **119** 158301
[14] Morris R G and Rogers T 2014 *J. Phys. A: Math. Theor.* **47** 342003

J. Stat. Mech. (2019) 063501

[15] Feller W 1968 *An Introduction to Probability Theory and its Applications* vol I (New York: Wiley)
[16] Redner S 2001 *A Guide to First-Passage Processes* (Cambridge: Cambridge University Press)
[17] Krapivsky P L and Redner S 2001 *Phys. Rev.* E **63** 066123
[18] 2018 Wolfram Research, Inc., Mathematica, Version 11.3
[19] Gillespie D T 1977 *J. Phys. Chem.* **81** 2340
[20] ben-Avraham D, Considine D, Meakin P, Redner S and Takayasu H 1990 *J. Phys. A: Math. Gen.* **23** 4297
[21] Korolev K S, Avlund M, Hallatschek O and Nelson D R 2010 *Rev. Mod. Phys.* **82** 1691
[22] Wilf H S 2005 *Generatingfunctionology* 3rd edn (Boca Raton, FL: CRC Press)

J. Stat. Mech. (2019) 063501