Large fluctuations in stochastic population dynamics: momentum-space calculations

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Abstract. Momentum-space representation provides an interesting perspective on the theory of large fluctuations in populations undergoing Markovian stochastic gain–loss processes. This representation is obtained when the master equation for the probability distribution of the population size is transformed into an evolution equation for the probability generating function. Spectral decomposition then yields an eigenvalue problem for a non-Hermitian linear differential operator. The ground-state eigenmode encodes the stationary distribution of the population size. For long-lived metastable populations which exhibit extinction or escape to another metastable state, the quasi-stationary distribution and the mean time to extinction or escape are encoded by the eigenmode and eigenvalue of the lowest excited state. If the average population size in the stationary or quasi-stationary state is large, the corresponding eigenvalue problem can be solved via the WKB approximation amended by other asymptotic methods. We illustrate these ideas in several model examples.

Keywords: stochastic particle dynamics (theory), population dynamics (theory), metastable states, large deviations in non-equilibrium systems

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1. Introduction

This work deals with the dynamics of populations experiencing intrinsic noise caused by the discreteness of individuals and the stochastic character of their interactions. When the average size $N$ of such a (stationary or quasi-stationary) population is large, the noise-induced fluctuations in the observed number of individuals are typically small, and only rarely large. In many applications, however, the rare large fluctuations can be very important. This is certainly true when their consequences are catastrophic, such as in the case of the extinction of an isolated self-regulating population after having maintained a long-lived metastable state, with applications ranging from population biology [1,2] and epidemiology [1,3] to genetic regulatory networks in living cells [4]. Another example of a catastrophic transition driven by a rare large intrinsic fluctuation is population explosion [5]. Rare large fluctuations may also induce stochastic switches between different metastable states [6]; these appear in genetic regulatory networks [7] and in other contexts. Less dramatic but still important examples involve large fluctuations in the rates of production of molecules on the surfaces of micron-sized dust grains in the interstellar medium, where the number of atoms participating in the chemical reactions can be relatively small [8,9]. As stochastic population dynamics is far from equilibrium and therefore defies treatment by standard methods of equilibrium statistical mechanics, large fluctuations of stochastic populations are of much interest to physics [10,11].

In this paper we consider single-species populations which are well mixed, so that spatial degrees of freedom are irrelevant. To account for the stochasticity of gain–loss processes (in the following—reactions) and the discreteness of the individuals (in the following—particles), we assume a Markov process and employ a master equation which describes the time evolution of the probability $P_n(t)$ of having a population size $n$ at (continuous) time $t$. If the population exhibits neither extinction nor a switch to another metastable state or to an infinite population size, a natural goal is to determine...
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the stationary probability distribution of the population size [12]. For metastable populations—populations experiencing either extinction or switches between different metastable states—one is usually interested in the mean time to extinction or escape (MTE), and in the long-lived quasi-stationary distribution (QSD) of the population size. For single-step processes these quantities can be calculated by standard methods. The MTE can be calculated exactly by employing the backward master equation [10,11]. This procedure yields an exact but unwieldy analytic expression for the MTE which, for a large population size in the metastable state, can be simplified via a saddle point approximation [13]. In its turn, the QSD of a single-step process can be found, in many cases, through a recursion.

For multi-step processes neither the MTE nor the QSD can be calculated exactly. Many practitioners have used, in different contexts of physics, chemistry, population biology, epidemiology, cell biology, etc, what is often called ‘the diffusion approximation’: an approximation of the master equation by a Fokker–Planck equation. The latter can be obtained via the van Kampen system size expansion, or other related prescriptions. With a Fokker–Planck equation at hand, the MTE and QSD can again be evaluated by standard methods [10,11]. Unfortunately, this approximation is in general uncontrolled, and fails in its description of the tails of the QSD. As a result, it gives exponentially large errors in the MTE [13]–[16].

Until recently, the MTE and QSD had been calculated accurately only for a few model problems involving multi-step processes. Recently, Escudero and Kamenev [17] and Assaf and Meerson [18] addressed a quite general set of reactions and developed controlled WKB approximations for the MTE and QSD for population switches [17] and population extinction [18]. When necessary, the WKB approximation must be supplemented by a recursive solution of the master equation at small population sizes [5,18], and by the van Kampen system size expansion in narrow regions where the ‘fast’ and ‘slow’ WKB modes are coupled and the WKB approximation fails [5,17,18].

The techniques developed in [17] and [18] (see also [5,6,15]) were formulated directly in the space of population size $n$. An alternative approach invokes a complementary space which can be interpreted as a momentum space. The momentum-space representation is obtained when the master equation—an infinite set of linear ordinary differential equations—is transformed into a single evolution equation—a linear partial differential equation—for the probability generating function $G(p,t)$. Here $p$, a complementary variable, is conjugate to the population size $n$ and plays the role of the ‘momentum’ in an effective Hamiltonian system which encodes, in the leading order of $1/N$ expansion, the stochastic population dynamics. One can then perform spectral decomposition of this linear partial differential equation for $G(p,t)$. In order to describe the stationary or metastable states, it suffices to consider the ground state and the lowest excited state of this spectral decomposition, whereas higher modes only contribute to short-time transients [16,19].

The ordinary differential equations for the ground state and the lowest excited state are determined by the specific set of reactions that the population undergoes. The order of these equations is equal to the highest order of inter-particle reactions. For example, for two-body (three-body) reactions the equations are of the second (third) order, etc. In general, these ordinary differential equations cannot be solved exactly, and some perturbation techniques, employing the small parameter $1/N \ll 1$, need to be used.
The momentum-space spectral theory was developed \cite{16,19,20} for two-body reactions. Here we extend the theory to any many-body reactions. We also determine, for the general case, the previously unknown boundary conditions for the above-mentioned eigenvalue problems. If there is no absorbing state at infinity, the boundary conditions are ‘self-generated’ by the demand that the probability generating function $G(p, t)$ be, at any $t$, an entire function on the complex plane $p$ \cite{21}. We show that, for two-body reactions, the population extinction problem can always be solved by matching the exact solution of a quasi-stationary equation for the lowest excited state (see below) with a perturbative solution of a non-quasi-stationary equation for the same state. This procedure always works when $N$ is sufficiently large. For reactions of three, four, … bodies the spectral decomposition can be used in conjunction with a $p$-space WKB (Wentzel–Kramers–Brillouin) approximation which employs the same small parameter $1/N$ but does not rely on the exact solution of the quasi-stationary equation. We find that there is a region of $p$ where the WKB approximation breaks down, and a region of $p$ where its accuracy is insufficient. In the former region a boundary layer solution can be found and matched with the WKB solution. In the latter region a simple non-WKB perturbative solution can be obtained. The theory extensions presented here turn the momentum-space spectral theory of large fluctuations into a more general tool.

As the evolution equation for $G(p, t)$ is equivalent to the master equation, the $p$-space approach is clearly advantageous, compared to the $n$-space approach, when the problem in the $p$ space admits an exact solution; see \cite{8,11}. Otherwise, the technical advantages of the $p$-space approach are not a priori obvious. In any case, it provides a viable alternative to, and an interesting perspective on, the theory of large fluctuations of stochastic populations.

Here is the layout of the rest of the paper. Section 2 briefly introduces the momentum-space spectral formalism, whereas in sections 3 and 4 we describe the methods of solution and illustrate them on several model examples. Section 3 deals with a well-studied prototypical chemical reaction scheme which describes a stationary production of hydrogen molecules on interstellar dust grains. Here we show that the WKB approximation not only gives accurate results for the production rate (including its fluctuations) of hydrogen molecules, but also yields a complete stationary probability distribution function of the number of hydrogen atoms, including its non-Gaussian tails. In section 4 we deal with isolated populations undergoing intrinsic-noise-driven extinction after maintaining a long-lived metastable state. Here, after some general arguments, we consider two different examples—one studied previously and one new—and determine the MTE and QSD. Throughout the paper we compare our analytical results with numerical solutions of the pertinent master equation and, when possible, with previous analytical results. Section 5 summarizes our findings and discusses the advantages and disadvantages of the $p$-space method compared with the ‘real-space’ WKB method \cite{5,6,15,17,18}.

2. The master equation, probability generating function and spectral formulation

Populations consist of discrete ‘particles’ undergoing stochastic gain and loss reactions. To account for both discreteness and stochasticity, we assume the Markov property (see
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e.g. \[10,11\]), and employ the master equation

\begin{equation}
\dot{P}_n(t) = \sum_{n' \neq n} W_{nn'} P_{n'} - W_{nn} P_n
\end{equation}

which describes the time evolution of the probability distribution function \(P_n(t)\) for having \(n\) particles at time \(t\). Here \(W_{nn'}\) is the transition rate matrix; it is assumed that \(P_{n<0} = 0\).

The probability generating function (see e.g. \[10,11\]) is defined as

\begin{equation}
G(p, t) = \sum_{n=0}^{\infty} p^n P_n(t).
\end{equation}

Here \(p\) is an auxiliary variable which is conjugate to the number of particles \(n\). Once \(G(p, t)\) is known, the probability distribution function \(P_n(t)\) is given by the Taylor coefficients

\begin{equation}
P_n(t) = \frac{1}{n!} \frac{\partial^n G}{\partial p^n} \bigg|_{p=0}
\end{equation}
or, alternatively, by employing the Cauchy theorem

\begin{equation}
P_n(t) = \frac{1}{2\pi i} \oint G(p, t) \frac{p^n}{p^{n+1}} dp,
\end{equation}

where the integration has to be performed over a closed contour in the complex \(p\) plane around the singular point \(p = 0\). For stochastic populations which do not exhibit population explosion \[5\], the probability \(P_n(t)\) decays faster than exponentially at large \(n\). Therefore, \(G(p, t)\) is an entire function of \(p\) on the complex \(p\) plane \[21\].

If the reaction rates are polynomial in \(n\), one can transform the master equation \(1\) into a single linear partial differential equation for the probability generating function,

\begin{equation}
\frac{\partial G}{\partial t} = \hat{L}G,
\end{equation}

where \(\hat{L}\) is a linear differential operator which includes powers of the partial differentiation operator \(\partial/\partial p\). Equation \(5\) is exact and equivalent to the master equation \(1\). If only one-body reactions are present, \(\hat{L}\) is of first order in \(\partial/\partial p\), and equation \(5\) can be solved by using characteristics \[11\]. For many-body reactions one can proceed by expanding \(G(p, t)\) in the as yet unknown eigenmodes and eigenvalues of the problem \[16,19,20\]:

\begin{equation}
G(p, t) = G_{st}(p) + \sum_{k=1}^{\infty} a_k \phi_k(p) e^{-E_k t}.
\end{equation}

As a result, the partial differential equation \(5\) is transformed into an infinite set of ordinary differential equations: for the (stationary) ground-state mode \(G_{st}(p)\) and for the eigenmodes of excited states \(\{\phi_k(p)\}_{k=1}^{\infty}\). By virtue of equation \(3\) or \(4\), the ground-state eigenmode determines the stationary probability distribution function of the system. If a long-lived population ultimately goes extinct, the stationary distribution is trivial: \(P_n = \delta_{n,0}\), where \(\delta_{n,0}\) is Kronecker’s delta. What is of interest in this case is the quasi-stationary distribution and its (exponentially long) decay time which yields an accurate approximation to the MTE. These quantities are determined by the lowest excited eigenmode \(\phi(p)\) and the eigenvalue \(E_1\), respectively \[16,19\]. The higher modes only contribute to short-time transients. Therefore, in the following we will focus on determining \(G_{st}\) or solving the eigenvalue problem for \(\phi_1(p)\) and \(E_1\).
3. Stationary distributions: ground-state calculations

As a first example, we consider a simple model of the production of H$_2$ molecules on micron-sized dust grains in an interstellar medium. This model was investigated by Green et al. [8], who computed the stationary probability distribution function for the number of hydrogen atoms via finding an exact solution to the ordinary differential equation for $G_{st}$. The same results were obtained, by a different method, by Biham and Lipshtat [9]. We will use this problem as a benchmark for the ground-state calculations using the momentum-space WKB approach. As we will see, this approach gives, for $N \gg 1$, an accurate approximate solution for $G_{st}(p)$, and so it can be employed with many other models where no exact solutions are available.

Consider the following set of reactions: absorption of H atoms by the grain surface $\emptyset \overset{\alpha}{\rightarrow} \text{H}$, desorption of H atoms, $\text{H} \overset{\beta}{\rightarrow} \emptyset$, and formation of H$_2$ molecules from pairs of H atoms which can be formally described as the annihilation $2\text{H} \overset{\gamma}{\rightarrow} \emptyset$.

To calculate the rate of production of H$_2$ molecules, one needs to determine the stationary probability distribution function of the H atoms, $P_n(t \rightarrow \infty)$. For convenience, we rescale time and reaction rates by the desorption rate $\beta$ and define $N = 2\beta/\gamma$ and $R = \alpha\gamma/(2\beta^2)$. Ignoring fluctuations, one can write down the following (rescaled) deterministic rate equation:

$$\dot{n} = NR - \bar{n} - \frac{2}{N} \bar{n}^2,$$

where $\bar{n}(t) \gg 1$ is the average population size. The only positive fixed point of this equation,

$$\bar{n} = \frac{N}{4}(\sqrt{1+8R} - 1),$$

is attracting, and the stationary probability distribution function $P_n$ is expected to be peaked around it. The master equation describing the stochastic dynamics of this system in rescaled time is

$$\frac{d}{dt}P_n(t) = \frac{1}{N}[(n+2)(n+1)P_{n+2}(t) - n(n-1)P_n(t)] + [(n+1)P_{n+1}(t) - nP_n(t)] + NR(P_{n-1} - P_n).$$

This yields the following partial differential equation for $G(p, t)$ [8]:

$$\frac{\partial G}{\partial t} = \frac{1}{N}(1 - p^2) \frac{\partial^2 G}{\partial p^2} + (1 - p) \frac{\partial G}{\partial p} + NR(p - 1)G.$$

The steady-state solution $G_{st}$ obeys the ordinary differential equation

$$\frac{1}{N}(1 + p)G_{st}'' + G_{st}' - NRG_{st} = 0,$$

where primes denote the $p$ derivatives. The boundary conditions are ‘self-generated’. Indeed, equality $G(p = 1, t) = 1$ holds at all times. This reflects conservation of probability; see equation (2). Therefore,

$$G_{st}(1) = 1.$$

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Furthermore, equation (11) has a singular point at \( p = -1 \). As \( G_{\text{st}}(p) \) must be analytic at \( p = -1 \), we demand
\[
G'_{\text{st}}(-1) - NRG_{\text{st}}(-1) = 0. \tag{13}
\]
The boundary value problem (11)–(13) is exactly solvable in special functions \[8\]. For a general set of reactions, however, one cannot expect an exact solution. Still, one can employ the small parameter \( 1/N \) to develop an accurate analytical approximation. To illustrate this point we will proceed as if we were unaware of the exact solution, and then compare the approximate solution with the exact one. As the small parameter \( 1/N \) appears in the coefficient of the highest derivative, it is natural to use (a dissipative variant of) the stationary WKB approximation in the \( p \) space \[20\]. The WKB ansatz is
\[
G_{\text{st}}(p) = a(p)e^{-NS(p)}, \tag{14}
\]
where the action \( S(p) \) and amplitude \( a(p) \) are non-negative functions of \( p \).

Using this ansatz in equation (10) with a zero left-hand side, we obtain
\[
\frac{1}{N}(1-p^2)[a'' - 2NS'a' - NS''a + N^2(S')^2a] + (1-p)(a' - NS'a - N Ra) = 0. \tag{15}
\]
In the leading order \( \mathcal{O}(N) \) we obtain a stationary Hamilton–Jacobi equation
\[
H[p, -S'(p)] = 0 \text{ with zero energy; cf \[22\].}
\]
The effective Hamiltonian is
\[
H(p, q) = (1-p)[(1+p)q^2 + q - R], \tag{16}
\]
where we have introduced \( q(p) = -S'(p) \); the reaction coordinate conjugate to the momentum \( p \). The trivial zero-energy phase orbit \( p = 1 \) is an invariant line of the Hamiltonian; it corresponds to the deterministic dynamics \[22\]. Indeed, the Hamilton’s equation for \( \dot{q} \),
\[
\dot{q} = R - q - 2q^2,
\]
coincides, in view of the relation \( q = n/N \), with the deterministic rate equation (7). Hamiltonian (16) also has two nontrivial invariant zero-energy lines which are composed of the two solutions, \( q_-(p) \) and \( q_+(p) \), of the quadratic equation \((1 + p)q^2 + q - R = 0\):
\[
q_-(p) = \frac{-1 - v(p)}{2(1 + p)}, \quad q_+(p) = \frac{-1 + v(p)}{2(1 + p)}. \tag{17}
\]
Here we have defined
\[
v(p) = \sqrt{1 + 4R(1 + p)}. \tag{18}
\]
The phase plane of this system is shown in figure 1. The phase orbit \( q = q_-(p) \) must be discarded. This is because \( q_-(p) \) diverges at \( p = -1 \), whereas \( G_{\text{st}}(p) \), and therefore \( S(p) \), must be analytic everywhere.

The remaining nontrivial zero-energy phase orbit \( q_+(p) \equiv q(p) \) has a special role. It describes the most probable path for the system to evolve along, (almost) with certainty, in the course of a fluctuation bringing the system from the fixed point \((1, q_1)\) in the phase space \((p, q)\) to a given point; see figure 1. Here \( q_1 = (1/4)(\sqrt{1 + 8R} - 1) \) is the attracting point of the deterministic rate equation; see equation (8).
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Figure 1. Molecular hydrogen production on a grain. Shown are zero-energy orbits of Hamiltonian (16) on the phase plane \((p, q)\). The thick solid line corresponds to the instanton \(q = q_+(p)\); see equation (17). The motion along the vertical line \(p = 1\) is described by the deterministic rate equation (7). The dashed lines depict the branch \(q = q_-(p)\). It is non-physical at \(q < 0\) and does not contribute to the WKB solution at \(q > 0\).

Integrating the equation \(S'(p) = -q_+(p)\), we obtain

\[
S(p) = -v(p) + v(1) + \ln \frac{v(p) + 1}{v(1) + 1},
\]

where we have fixed the definitions of \(a(p)\) and \(S(p)\) by demanding \(S(p = 1) = 0\).

To calculate the amplitude \(a(p)\) we proceed to the subleading \(O(1)\) order in equation (15):

\[
-2(1 + p)S'a' - (1 + p)S''a + a' = 0.
\]

Using \(S(p)\) from equation (19), we arrive at a first-order ordinary differential equation for \(a(p)\),

\[
\frac{a'(p)}{a(p)} = \frac{4R^2(1 + p)}{v(p)^2[1 + v(p)]^2}.
\]

Solving this equation, we obtain the WKB solution

\[
G_{\text{st}}^{WKB}(p) = \frac{v(1)^{1/2}[1 + v(p)]}{v(p)^{1/2}[1 + v(1)]} e^{-NS(p)},
\]

where the integration constant is chosen so as to obey boundary condition (12). As one can easily check, the WKB solution (22) also obeys boundary condition (13).

As expected, the pre-exponent \(a(p)\) of the WKB solution (22) diverges at the turning point \(p_T = -1 - 1/(4R) < -1\) of the zero-energy phase orbit; see figure 1. As a result, the WKB solution breaks down in the close vicinity of this point. At \(p < p_T\), a WKB solution of a different nature appears: it exhibits decaying oscillations as a function of \(p\). The

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oscillating WKB solution can be found by treating $S(p)$ as a complex-valued, rather than
real, function. We will not need the oscillating solution, because the non-oscillating one, equation (22), turns out to be sufficient for the purpose of calculating the probabilities $P_n$; see below.

Now we can compare the WKB solution (22) with the exact solution of the problem (11)–(13), derived by Green et al [8]:

$$G_{\text{exact}}(p) = \left(\frac{2}{1+p}\right)^{(N-1)/2} \frac{I_{N-1}[2N\sqrt{R(1+p)}]}{I_{N-1}(2N\sqrt{2R})},$$  

(23)

where $I_k(w)$ is the modified Bessel function. To this end let us calculate the large-$N$ asymptote of $I_{N-1}[2N\sqrt{R(1+p)}]$ by using the integral definition of the modified Bessel function [23]

$$I_{N-1}[2N\sqrt{R(1+p)}] = \frac{[N^2R(1+p)]^{(N-1)/2}}{\sqrt{\pi}\Gamma(N-1/2)} \int_{-1}^{1} \frac{(1-t^2)^N e^{-2N\sqrt{R(1+p)t}}}{(1-t^2)^{3/2}} dt,$$

(24)

where $\Gamma(\cdots)$ is the Euler Gamma function. As $N \gg 1$, we can evaluate the integral by using the saddle point approximation [24]. Defining $f(t) = \ln(1-t^2) - 2\sqrt{R(1+p)t}$, we find the relevant saddle point

$$t_*(p) = \frac{1 - \sqrt{1 + 4R(1+p)}}{2\sqrt{R(1+p)}} = -\sqrt{\frac{v(p) - 1}{v(p) + 1}},$$

with $v(p)$ from equation (18). Then, expanding $f(t) \simeq f(t_*) + (1/2)f''(t_*)(t - t_*)^2$ with $f''(t_*) = -v(p)[1 + v(p)]$, and performing the Gaussian integration, we obtain the $N \gg 1$ asymptote

$$I_{N-1}[2N\sqrt{R(1+p)}] \simeq \frac{1 + v(p)}{2\sqrt{2\pi}\Gamma(N-1/2)\sqrt{Nv(p)}} \times [N^2R(1+p)]^{(N-1)/2} e^{N(v(p)-1)\ln 2 - \ln[1+v(p)]}. $$

(25)

Note that the saddle point approximation is valid on the entire segment $-1 \leq p \leq 1$. In particular, equation (25) with $p = 1$ yields the $N \gg 1$ asymptote of the denominator of equation (23). Now one can see that the large-$N$ asymptote of equation (23) exactly coincides with the WKB solution (22). Actually, the WKB result is indistinguishable from the exact result already for $N = 10$; see figure 2.

Of a primary interest in the context of astrochemistry are the mean and variance of the steady-state rate of production of H$_2$ molecules. Going back to physical units, we can write the mean steady-state production rate as

$$\mathcal{R}(H_2) = \frac{N}{2} \sum_{n=1}^{\infty} n(n-1)P_n = \frac{\gamma}{2} (n(n-1)) = \frac{\gamma}{2} G_{\text{st}}''(1),$$

$$\mathcal{R}(H_2) \simeq \frac{2\gamma N^2 R^2}{[v(1) + 1]^2} \left[1 - \frac{1}{Nv^2(1)}\right],$$

(26)

where $v(p)$ is given by equation (18). One can check that this expression coincides with that obtained from the exact result (see equation (22) in [8]) in the leading and subleading
order at $N \gg 1$. The leading term in equation (26) is what the deterministic rate equation (7) predicts.

Now consider the variance of the steady-state production rate of $H_2$ molecules:

$$V(H_2) = \frac{\gamma^2}{2} \left[ \langle n^2(n-1)^2 \rangle - \langle n(n-1) \rangle^2 \right].$$

Using the identity

$$n^2(n-1)^2 = n(n-1)(n-2)(n-3) + 4n(n-1)(n-2) + 2n(n-1),$$

we obtain the exact relation

$$V(H_2) = \frac{\gamma^2}{2} \left\{ G^{IV}(1) + 4G'''(1) + 2G''(1) - [G''(1)]^2 \right\}.$$

From WKB solution (22) we obtain in the leading order

$$V(H_2) \simeq \frac{16\gamma N^3 R^3}{v(1)[v(1) + 1]^4} \left[ v(1) + 6R + 1 \right].$$

The relative fluctuations of the production rate, $\sqrt{V/R}$, scale with $N$ as $N^{-1/2}$, as expected.

Actually, the WKB approximation yields the whole stationary probability distribution function of the number of H atoms. Green et al [8] obtained this distribution exactly from equations (23) and (3):

$$P_n = 2^{(N-1)/2} \frac{(N^2 R)^{n/2}}{n!} \frac{I_{N+n-1}(2N\sqrt{R})}{I_{N-1}(2N\sqrt{2R})}. \quad (28)$$

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The $N \gg 1$, $n \gg 1$ asymptote of (28) can be written as
\[ P_n \simeq \frac{\sqrt{(1 + q)v(1)} + u(q)}{\sqrt{2\pi qNu(q)} + v(1)} \times e^{N\ln[1 + v(1)] - v(1) + q + (1 + q)u(q) - \ln[(1 + q)(1 + u(q))]} - q ln[q(1 + q)(1 + u(q))/2R)], \tag{29} \]
where $q = n/N$, $v(p)$ is given by equation (18) and
\[ u(q) = \sqrt{1 + 4R/(1 + q)^2}. \tag{30} \]
Now we compare equation (29) with the WKB result, obtained from equations (4) and (22):
\[ P_n^{\text{WKB}} = \frac{1}{2\pi i} \oint dp \frac{v(1)^{1/2}[1 + v(p)]}{p v(p)^{1/2}[1 + v(1)]} e^{-NS(p) - n \ln p}, \tag{31} \]
where $S(p)$ is given by equation (19). As $n \gg 1$, we can evaluate the integral via the saddle point approximation. Let $f(p) = -NS(p) - n \ln p$. The saddle point is at $p_s = q(1 + q)(1 + u(q))/2R$, where $u(q)$ is given by equation (30). As $f''(p_s) > 0$, the integration contour in the vicinity of the saddle point must be chosen perpendicular to the real axis. This adds an additional phase of $e^{i\pi/2}$ to the solution [24], which cancels $i$ in the denominator of equation (31). After the Gaussian integration and some algebra, equation (31) coincides with equation (29). Finally, one can calculate $P_n$ at $N \gg 1$ but $n = O(1)$ by directly differentiating the WKB result (22) for $G_{\text{st}}(p)$; see equation (3). The resulting probability distribution function is shown in figure 3. As one can see, the agreement between the WKB distribution and the exact distribution is excellent for all $n$.

4. Metastability and extinction: first-excited-state calculations

Now we switch to isolated stochastic populations, so that there is no influx of particles into the system. If there is no population explosion, isolated populations ultimately undergo extinction with probability 1. The deterministic rate equation for such a population can be written as
\[ \dot{n} = \bar{n}\psi(\bar{n}), \tag{32} \]
where $\psi(\bar{n})$ is a smooth function. In the following we assume $\psi(0) > 0$, so $\bar{n} = 0$ is a repelling fixed point of equation (32). The deterministically stable population size corresponds to an attracting fixed point $\bar{n} = n_1 > 0$. According to the classification of [18], such populations exhibit scenario A of extinction.

Let $n_1 = O(N) \gg 1$. After a short relaxation time $t_r$, the population typically converges into a long-lived metastable state whose population size distribution is peaked around $n = n_1$. This metastable probability distribution function is encoded in the lowest excited eigenmode $\phi(p) \equiv \phi_1(p)$ of the probability generating function $G(p, t)$ (6). Indeed, at $t \gg t_r$, the higher eigenmodes in the spectral expansion (6) have already decayed, and $G(p, t)$ can be approximated as [16, 19]
\[ G(p, t) \simeq 1 - \phi(p)e^{-Et}, \tag{33} \]
where the lowest excited eigenfunction is normalized so that $\phi(0) = 1$. The (exponentially small) lowest excited eigenvalue $E \equiv E_1$ determines the MTE of the population, $E \simeq \tau_{\text{ex}}^{-1}$.
Figure 3. Molecular hydrogen production on a grain. Shown is the natural logarithm of the stationary distribution $P_n$ versus $n$ for $N = 50$ and $R = 1$. The solid line is the WKB approximation (29), the dashed line is the exact solution (28), and the dash–dotted line is the Gaussian approximation. The WKB approximation and the exact solution are indistinguishable for all $n$. The non-Gaussian tails of the distribution cannot be described correctly through the van Kampen system size expansion. The inset shows, with different symbols, the small-$n$ asymptote of the distribution obtained analytically and numerically.

The slowly time-dependent probability distribution function of the population size, at $t \gg t_r$, is

$$P_{n>0}(t) \simeq \pi_n e^{-t/\tau_{ex}}, \quad P_0(t) \simeq 1 - e^{-t/\tau_{ex}}.$$ (34)

That is, the metastable probability distribution function decays exponentially slowly in time, whereas the extinction probability $P_0(t)$ grows exponentially slowly and reaches 1 at $t \to \infty$. The shape function $\pi_n$ of the metastable distribution is called the quasi-stationary distribution (QSD). The QSD and MTE of a metastable population can be obtained by solving the eigenvalue problem for $\phi(p)$ and $E$, respectively. We now discuss some general properties of the solution to this eigenvalue problem, whereas in the following subsections we will illustrate the method of solution on two examples.

4.1. General considerations

Plugging equation (33) into (5), we arrive at an ordinary differential equation for $\phi(p)$:

$$\hat{L} \phi + E \phi = 0.$$ (35)

As $G(p, t)$ is an entire function on the complex $p$ plane [21], $\phi(p)$ must be analytic at all singular points of the differential operator $\hat{L}$. If the order of this operator is $K$, this demand yields $K$ ‘self-generated’ boundary conditions for $\phi(p)$. In view of the equality $G(p = 1, t) = 1$, operator $\hat{L}$ vanishes at $p = 1$, which yields a universal boundary condition:
\(\phi(1) = 0\). The rest of the \(K - 1\) self-generated boundary conditions are problem specific; see examples below.

What is the general structure of differential operator \(\hat{L}\)? For populations that experience extinction, \(\hat{L}\phi\) cannot include a term proportional to \(\phi\), as such a term would correspond to an influx of particles into the system, \(\emptyset \rightarrow A\), and would prevent extinction. In general, \(\hat{L}\) includes first-order derivative terms (corresponding to branching and decay processes) and higher order derivative terms. For extinction scenario A one has \(\psi(0) > 0\); see equation (32). Let \(b_0\) denote the rate of decay \(A \rightarrow \emptyset\), and \(b_m\), \(m = 2, 3, \ldots, M\), denote the rates of branching reactions \(A \rightarrow mA\). One has \(\psi(0) \equiv b_2 + 2b_3 + \cdots + (M-1)b_M - b_0 > 0\). Rescaling time by \(\psi(0)\), we see that the (rescaled) coefficient of the term \(\tilde{n}^j\) (for \(j = 1, 2, \ldots\)) in equation (32) must scale as \(N^{1-j}\) to ensure that \(n_1 = \mathcal{O}(N)\). As a result, the (rescaled) coefficient of the \(j\)th-order derivative term in \(\hat{L}\) scales as \(N^{1-j}\), and \(\hat{L}\) can be written as

\[
\hat{L} = f_1(p) \frac{d}{dp} + \frac{1}{N} f_2(p) \frac{d^2}{dp^2} + \cdots + \frac{1}{N^{K-1}} f_K(p) \frac{d^K}{dp^K}.
\]

For reaction rates that are polynomial in \(n\), the functions \(f_j(p)\) are polynomial in \(p\). Notably, all functions \(f_j(p)\) vanish at \(p = 1\). What does the solution of equation (35) look like at \(N \gg 1\)? As \(E\) turns out to be exponentially small in \(N\), the simplest approximation for equation (35) would be to discard all terms except \(f_1(p)\frac{d\phi}{dp}\), arriving at a constant solution \(\phi(p) = 1\) (according to our choice of normalization). Indeed, as \(n_1 = \mathcal{O}(N)\) \(\gg 1\), the probability of observing \(n \ll n_1\) particles in the metastable state is exponentially small. These probabilities are proportional to low order derivatives of \(\phi\) at \(p = 0\) (see equations (3) and (33)), so \(\phi(p)\) must indeed be almost constant there. This solution, however, does not obey the zero boundary condition at \(p = 1\). The true solution, therefore, must rapidly fall to 0 in the close vicinity of \(p = 1\); see figure 4. The point \(p = 1\) is a singular point of equation (35). Actually, when approaching \(p = 1\) from the left, the almost constant solution breaks down even earlier—in the vicinity of another point \(p = p_f < 1\) where \(f_1(p)\) vanishes; see the next paragraph. In the vicinity of \(p = p_f\), the first-order derivative term ceases to be dominant, and all terms in equation (35), including \(E\phi\), are comparable. Although \(\phi(p)\) deviates from a constant value in the vicinity of \(p = p_f\), one can still treat this deviation perturbatively: \(\phi(p) \approx 1 + \delta\phi(p)\), where \(\delta\phi \ll 1\). When \(p\) becomes distinctly larger than \(p_f\), \(\phi(p)\) already varies strongly. Here, the \(E\phi\) term (which comes from the time derivative of \(G(p, t)\)) can again be neglected, and so the (nontrivial) solution which is sought in this region is quasi-stationary. The quasi-stationary solution can be found in the WKB approximation, as the typical length scale \(1/N\), over which \(\phi(p)\) varies, is much smaller here than \(1 - p_f\) (a more accurate criterion will appear later).

Why does the root \(p_f\) of function \(f_1(p)\) exist? After some algebra, function \(f_1(p)\) can be written as

\[
f_1(p) = \sum_{m=0}^{M} \hat{b}_m (p^m - p),
\]

where \(\hat{b}_m = b_m/\psi(0)\). The polynomial equation \(f_1(p) = 0\) has appeared in the context of the \(n\)-space description of stochastic population extinction \[18\]. It has been shown in \[18\] that this equation has exactly two real roots: \(p = 1\) and \(p_f\), where in general \(0 \leq p_f < 1\).
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Figure 4. Shown is a sketch of the eigenfunction \( \phi(p) \) of the lowest excited state at \( N \gg 1 \) for a typical problem of population extinction. \( \phi(p) \) is almost constant on the region \( p < 1 \) except close to \( p = 1 \), where it rapidly goes to zero.

Now we can summarize the general scheme of solution of the eigenvalue problem for the lowest excited state. One has to consider three separate regions: (i) the region to the left of, and sufficiently far from, the point \( p = p_f \), where one can put \( \phi(p) = 1 \) up to exponentially small corrections, (ii) in the boundary layer region \( |p - p_f| \ll p_f \) where \( \phi(p) \) is still very close to 1 and can be sought perturbatively, and (iii) in the quasi-stationary region \( p_f < p \leq 1 \), where \( \phi(p) \) varies strongly, and the WKB approximation can be used. The solutions in the neighboring regions can be matched in their regions of joint validity. This procedure holds, at \( N \gg 1 \), for a broad class of systems exhibiting extinction.

There is a convenient shortcut to this general procedure when the highest order reaction in the problem is a two-body one. Here the quasi-stationary equation (equation (35) with the \( E\phi \) term neglected) is always solvable exactly. There is no need to apply the WKB approximation in such cases, and it suffices to consider just two, rather than three, regions; see the next subsection. Finally, regardless of the order of \( \hat{L} \), it is simpler to deal with \( u(p) \equiv \phi'(p) \) than with \( \phi(p) \) itself, as this enables one to reduce the order of the ordinary differential equation by 1 everywhere.

4.2. Branching, annihilation and decay

The first example deals with a population of ‘particles’ which undergoes three stochastic reactions: branching \( A \xrightarrow{\lambda} 2A \), decay \( A \xrightarrow{\mu} \emptyset \) and annihilation \( 2A \xrightarrow{\sigma} \emptyset \). As the state \( n = 0 \) is absorbing, the population ultimately goes extinct. This example was solved by Kessler and Shnerb [15] via ‘real-space’ WKB approximation, where the calculations are done in the space of population size. Here we solve it in the momentum space. Because of the presence of the linear decay reaction \( A \to 0 \), this example exhibits a generic transcritical bifurcation as a function of the control parameter \( R_0 \) introduced below, and generalizes simple single-parameter models [16, 19] considered earlier. The deterministic rate equation reads

\[
\dot{n} = (\lambda - \mu)n - \sigma n^2.
\]
For $\lambda > \mu$ equation (38) has, in addition to the trivial fixed point $\bar{n} = 0$, also a positive fixed point $n_1 = (\lambda - \mu)/\sigma$. When starting from any $\bar{n}(t = 0) > 0$, the population size flows to the attracting fixed point $\bar{n} = n_1$, with characteristic relaxation time $t_r = (\lambda - \mu)^{-1}$, and stays there forever. On rescaling time, $\lambda t \to t$, and introducing rescaled parameters, $N = \lambda/\sigma$ and $R_0 = \lambda/\mu$, the attracting fixed point becomes $n_1 = N(1 - R_0^{-1})$. We demand that $N \gg 1$, and $R_0 > 1$ and not too close to 1 (the exact criterion will appear later).

When $R_0$ exceeds 1 the deterministic system undergoes a transcritical bifurcation.

To account for intrinsic noise we consider the master equation
\[
\frac{d}{dt} P_n(t) = \frac{1}{2N} [(n + 2)(n + 1)P_{n+2}(t) - n(n - 1)P_n(t)] + (n - 1)P_{n-1}(t) - nP_n(t) \\
+ \frac{1}{R_0}[(n + 1)P_{n+1} - nP_n], 
\] (39)

where time is rescaled, $\lambda t \to t$. The evolution equation for the probability generating function $G(p, t)$ is
\[
\frac{\partial G}{\partial t} = \frac{1}{2N}(1 - p^2) \frac{\partial^2 G}{\partial p^2} + (p - 1) \left(p - \frac{1}{R_0}\right) \frac{\partial G}{\partial p}. 
\] (40)

At $t \gg t_r = (1 - 1/R_0)^{-1}$ the metastable probability distribution function, peaked at $n \simeq n_1$, sets in, and equation (33) holds. To determine the QSD and MTE we turn to the Sturm–Liouville problem for the lowest excited eigenmode $\phi(p)$ and eigenvalue $E$:
\[
\frac{1}{2N}(1 - p^2)\phi'' + (p - 1) \left(p - \frac{1}{R_0}\right) \phi' + E\phi = 0. 
\] (41)

Here, the self-generated boundary conditions for $\phi(p)$ are $\phi(1) = 0$ and $2(1 + R_0^{-1})\phi'(-1) + E\phi(-1) = 0$. Because of the expected exponential smallness of $E$, the latter condition can be safely approximated by $\phi'(-1) \simeq 0$.

We now apply the procedure of solution presented in the previous subsection to equation (41). Using $u(p) = \phi'(p)$, the exact solution of the quasi-stationary equation (equation (41) without the $E\phi$ term),
\[
\frac{1}{2N}(1 - p^2)u' + (p - 1) \left(p - \frac{1}{R_0}\right) u = 0, 
\] (42)

can be written as
\[
u(p) = C e^{-NS(p)}. 
\] (43)

Here
\[
S(p) = 2 \left[1 - p + \left(1 + \frac{1}{R_0}\right) \ln \left(\frac{1 + p}{2}\right)\right]. 
\] (44)

To determine the arbitrary constant $C$ we need a boundary condition for $u(p)$ at $p = 1$. It follows from equation (33) that, at $t \gg t_r$,
\[
\frac{\partial G}{\partial p}(1, t) \simeq -u(1)e^{-Et}. 
\] (45)
On the other hand, by virtue of equation (2), the left-hand side of equation (45) is equal to \( \dot{n}(t) \) which behaves as \( n_1 \exp(-Et) \); see e.g. [16]. As a result, \( u(1) \approx -n_1 \) and, by using equation (43), we obtain \( C = -N(1 - R_0^{-1}) \). Therefore,

\[
    u(p) = -N \left( 1 - \frac{1}{R_0} \right) e^{-NS(p)}
\]

(46)

with \( S(p) \) from equation (44). This yields the solution that we looked for: \( \phi = \int_1^p u(s) \, ds \), which satisfies the boundary condition \( \phi(1) = 0 \). One can check now that neglecting the \( E\phi \) term in equation (41) demands \( pR_0 - 1 \gg N^{-1/2} \).

Although there is no need in the WKB approximation in this case of a two-body reaction, it is still instructive to re-derive equation (46) by using the WKB approximation for \( \phi(p) \). To this end we consider the quasi-stationary version of equation (41),

\[
    \frac{1}{2N} (1 - p^2) \phi'' + (p - 1) \left( p - \frac{1}{R_0} \right) \phi' = 0,
\]

(47)

and make a WKB ansatz \( \phi(p) = a(p) \exp[-NS(p)] \). In the leading order in \( N \gg 1 \) we obtain a stationary Hamilton–Jacobi equation \( H[p, -S'(p)] = 0 \) with effective Hamiltonian [25]

\[
    H(p, q) = \left[ p - \frac{1}{R_0} - \frac{(1 + p)q}{2} \right] q(p - 1).
\]

(48)

Here, as in section 3, \( q(p) = -S'(p) \) is the reaction coordinate conjugate to the momentum \( p \). There are two trivial zero-energy orbits of this Hamiltonian: the deterministic orbit \( p = 1 \) and the ‘extinction orbit’ \( q = 0 \). The action along the extinction orbit is zero: \( S(p) = 0 \), so the corresponding WKB mode can be called ‘slow’. There is also a nontrivial zero-energy orbit \( q(p) = 2(p - R_0^{-1})/(1 + p) \). It includes a heteroclinic orbit exiting, at \( t = -\infty \), the fixed point \((p = 1, q = q_1 \equiv n_1/N)\) and entering, at \( t = \infty \), the fixed point \((p = R_0^{-1}, q = 0)\) of the phase plane \((p, q)\); see figure 5. This orbit is the ‘extinction instanton’ [22,25]. It describes the most probable path of the system from the long-lived metastable state to extinction. Integrating along this orbit and choosing \( S(p = 1) = 0 \), we recover equation (44). This solution can be called the ‘fast’ WKB mode.

In the subleading order of the WKB approximation one obtains \( a(p) = (1 - R_0^{-1})(1 + p)/[2(p - R_0^{-1})] \) for the fast WKB mode and \( a(p) = \text{const} \) for the slow one. The general WKB solution is a superposition of the two modes,

\[
    \phi(p) = 1 - \frac{(1 - R_0^{-1})(1 + p)}{2(p - R_0^{-1})} e^{-NS(p)}
\]

(49)

with \( S(p) \) from equation (44). Here we have already imposed the boundary condition \( \phi(1) = 0 \) and normalization condition \( \phi(0) \approx 1 \). The \( p \) derivative of \( \phi(p) \) from equation (49) yields, in the leading order, equation (46). As is clear from equation (49), the WKB solution breaks down in the vicinity of the point \( p = R_0^{-1} \), where the slow and fast WKB modes become strongly coupled. Here the quasi-stationarity does not hold.

We now proceed, therefore, to the non-quasi-stationary region \(-1 \leq p \lesssim p_f \) (a more restrictive condition will appear \textit{a posteriori}). It is easier to deal with it in terms of \( u(p) \), rather than \( \phi(p) \). Here we can treat the \( E\phi \) term in equation (41) perturbatively:
Figure 5. Branching, annihilation and decay. Shown are zero-energy lines of Hamiltonian (48) on the \((p, q)\) phase plane. The thick solid line corresponds to the instanton \(q = -S'(p)\) (44). Here \(q_1 = n_1/N = 1 - R_0^{-1}\), and the area of the shaded region is equal to \(S_0\) from equation (55).

\(\phi(p) = 1 + \delta\phi(p)\), where \(\delta\phi \ll 1\) [16,19]. As a result, equation (41) becomes an inhomogeneous first-order equation for \(u(p) = \delta\phi'(p)\):

\[
\frac{1}{2N}(1 - p^2)u' + (p - 1)\left(p - \frac{1}{R_0}\right)u = -E,
\]

which can be solved by variation of parameter. For two-body reactions the corresponding homogeneous equation, which coincides with the quasi-stationary equation (42), is exactly solvable. As a result, one can solve equation (50) in the entire non-quasi-stationary region which includes both \(p < p_f\) and \(|p - p_f| \ll p_f\). The solution is

\[
u(p) = -2NEe^{2N[p-(1+1/R_0)\ln(1+p)]} \int_{-1}^{p} \frac{\exp\{2N[s-(1+1/R_0)\ln(1+s)]\}}{1-s^2} ds,
\]

where the arbitrary constant is chosen so as to obey the boundary condition \(u(-1) \simeq 0\). Note, that the integrand in equation (51) is regular at \(s = -1\), so the perturbative solution is well-behaved. Solution (51) remains valid as long as \(\phi\) is close to 1. As one can check, this holds for \(1 - p \gg N^{-1/2}\), cf [16,19]. The perturbative solution (51) can be matched with the quasi-stationary solution (46), e.g. at \(N^{-1/2} \ll pR_0 - 1 \ll 1\).

Solution (51) simplifies in the ‘left region’ \(p < p_f\), not too close to \(p_f\). By Taylor expanding the integrand in equation (51) (which is a monotone increasing function of \(p\) for \(p < p_f\)) in the vicinity of \(s = p\), we obtain

\[
u(p)^{\text{left}} \simeq -\frac{E}{(p - 1)(p - R_0^{-1})}.
\]

This result (which holds in the region \(1 - pR_0 \gg N^{-1/2}\)) has a simple meaning: here the first-derivative term in equation (50) is negligible. Neglecting this term in equation (50) (or

---

\(^4\) The joint region of (46) and (51) is actually broader and spans from \(pR_0 - 1 \gg N^{-1/2}\) to \(1 - p \gg N^{-1/2}\).
the term proportional to \( \phi''(p) \) in equation (41)) is the same as disregarding the two-body reaction \( 2A \rightarrow \emptyset \) compared with the one-body reactions of branching and decay. This is indeed a legitimate approximation at small \( n \) [15, 18]. Note that, not too close to \( p = p_f \), \( u(p) \) left is exponentially small in \( N \), so \( \phi \approx 1 \) up to an exponentially small correction. Putting \( \phi = 1 \) in the left region, however, would be too crude an approximation, as it would only give a trivial left tail of the QSD: \( \pi_1 = \pi_2 = \cdots = 0 \). Correspondingly, the solution in the left region cannot be obtained from the WKB approximation.

We can now find the eigenvalue \( E \) by matching the quasi-stationary solution (46) and the perturbative non-quasi-stationary solution (51) in their joint validity region \( N^{-1/2} \ll pR_0 - 1 \ll 1 \) (see footnote 4). For \( pR_0 - 1 \gg N^{-1/2} \), the integral in equation (51) can be evaluated by using the saddle point approximation. The saddle point is at \( p = p_f = R_0^{-1} \), and the result is

\[
u(p) \approx -\frac{2E\sqrt{\pi}NR_0^{3/2}}{\sqrt{R_0 + 1}(R_0 - 1)} e^{-2N[1/R_0-(1+1/R_0)\ln(1+1/R_0)]+2N[p-(1+1/R_0)\ln(1+p)].} \tag{53}\]

Matching this result with the quasi-stationary solution (46), we find

\[
E = \sqrt{\frac{N(R_0 + 1)(R_0 - 1)^2}{4\pi R_0^{3/2}}} e^{-NS_0}, \tag{54}
\]

where

\[
S_0 = 2 \left[ 1 - \ln 2 - \frac{1+\ln 2}{R_0} + \left( 1 + \frac{1}{R_0} \right) \ln \left( 1 + \frac{1}{R_0} \right) \right]. \tag{55}
\]

The MTE, in physical units, is \( \tau_{ex} = (\lambda E)^{-1} \) with \( E \) from equation (54), in agreement with [15]. As \( R_0 \rightarrow \infty \) the decay reaction \( A \rightarrow 0 \) becomes irrelevant, and one recovers the result for the branching and annihilation model [15, 16, 26]. When \( R_0 - 1 \ll 1 \), the system is close to the transcritical bifurcation of the deterministic rate equation. The corresponding asymptote of equation (54),

\[
E = \sqrt{\frac{N}{2\pi}} (R_0 - 1)^2 e^{-(N/2)(R_0 - 1)^2},
\]

is valid when \( R_0 - 1 \gg N^{-1/2} \), so \( E \) is still exponentially small in \( N \).

Having found \( E \), we have a complete solution for \( u(p) \), given by equations (46) and (51). Now one can find the QSD by using equation (3) for \( n = \mathcal{O}(1) \) and equation (4) for \( n \gg 1 \). The results coincide with those obtained by Kessler and Shnerb [15] by using the ‘real-space’ WKB approximation, so we will not present them here. The large-\( n \) tail of the QSD decays faster than exponentially, thus justifying our a priori assumption that \( \phi(p) \) is an entire function in the complex \( p \) plane. Shown in figure 6 is a comparison between the analytical and numerical solutions for \( \partial_p G \simeq -u(p)e^{-Et} \) at a time \( t_e \ll t \ll 1/E \), when \( \partial_p G \simeq -u(p) \).

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Figure 6. Branching, annihilation and decay. Shown is the $p$ derivative $\partial_p G$ of the probability generating function $G$ at $t_r \ll t \ll 1/E$ for $N = 10^3$ and $R_0 = 1.5$. The solid line is the absolute value of the perturbative solution (51); the dashed line is the absolute value of the quasi-stationary solution (46). In their region of joint validity the two lines are indistinguishable. The crosses indicate the values obtained by a numerical solution of equation (40) for $n_0 = 20$ particles at $t = 0$ and boundary conditions $G(1, t) = 1$ and $\partial_p G(-1, t) = 0$.

4.3. Branching and triple annihilation

Here we again consider a metastable population on the way to extinction, but now a three-body reaction is present. Our model system includes two reactions: the branching $A \xrightarrow{\lambda} 2A$ and the triple annihilation $3A \xrightarrow{\mu} \emptyset$. The deterministic rate equation,

$$\dot{\bar{n}} = \lambda \bar{n} - \frac{\mu}{2} \bar{n}^3,$$

has two relevant fixed points: the repelling point $n = 0$ and the attracting point $n_1 = (2\lambda/\mu)^{1/2} \equiv N \gg 1$. According to equation (56), the system size approaches $\bar{n} = n_1$ after the relaxation time $t_r = \lambda^{-1}$, and stays there forever. Contrary to this prediction, fluctuations drive the population to extinction. Upon rescaling time $t \to \lambda t$, the master equation reads

$$\frac{dP_n(t)}{dt} = (n - 1)P_{n-1} - nP_n + \frac{1}{3N^2}[(n + 3)(n + 2)(n + 1)P_{n+3}$$

$$- n(n - 1)(n - 2)P_n],$$

(57)

whereas the evolution equation for $G(p, t)$ is

$$\frac{\partial G}{\partial t} = \frac{1}{3N^2}(1 - p^3)\frac{\partial^3 G}{\partial p^3} + p(p - 1)\frac{\partial G}{\partial p}.$$  

(58)

At $t \gg t_r$, equation (33) holds, and the ordinary differential equation for the lowest excited eigenfunction $\phi(p)$ is

$$\frac{1}{3N^2}(1 - p^3)\phi''' + p(p - 1)\phi' + E\phi = 0.$$  

(59)

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This equation has three singular points in the complex $p$ plane. These are the roots of $1 - p^3$: one real, $p_1 = 1$, and two complex, $p_2 = e^{2\pi i / 3}$ and $p_3 = e^{4\pi i / 3}$. Since $\phi(p)$ must be analytical at all these points, $\phi(p)$ must satisfy three conditions:

$$p_i(p_i - 1)\phi'(p_i) + E\phi(p_i) = 0 \quad i = 1, 2, 3.$$  \hfill (60)

Here the $p$ derivative is in the complex plane. For $i = 1$ equation (60) yields $\phi(p) = 1$. As $E$ turns out to be exponentially small in $N \gg 1$, we can neglect small terms proportional to $E$ in the conditions for $i = 2$ and 3 and obtain $\phi'(p = e^{2\pi i / 3}) \simeq 0$ and $\phi'(p = e^{4\pi i / 3}) \simeq 0$.

In the quasi-stationary region (the exact location of which will be determined later) equation (59) becomes

$$\frac{1}{3N^2}(1 - p^3)\phi'' + p(p - 1)\phi' = 0.$$  \hfill (61)

This equation is of second order for $u(p) = \phi'(p)$, but it is not exactly solvable in terms of known special functions, and this is a typical situation for three-body, four-body, ... reactions. The presence of the large parameter $N \gg 1$ justifies the WKB ansatz $\phi(p) = a(p)e^{-NS(p)}$. It yields, in the leading order of $N \gg 1$, a stationary Hamilton–Jacobi equation $H[p, -S'(p)] = 0$ with Hamiltonian

$$H(p, q) = \left[ p - \frac{(1 + p + p^2)q^2}{3} \right] q(p - 1).$$  \hfill (62)

Here again, in addition to the trivial zero-energy lines $q = 0$ and $p = 1$, one obtains an instanton orbit

$$q = \psi(p) \equiv \left( \frac{3p}{1 + p + p^2} \right)^{1/2}$$  \hfill (63)

which connects the fixed points $(1, q_1 = n_1 / N = 1)$ and $(0, 0)$ in the $(p, q)$ plane; see figure 7. The instanton corresponds to the fast-mode WKB solution, whereas the orbit $q = 0$ corresponds to the slow-mode WKB solution, like for the previous example.

Again, it is simpler to do the actual calculations for $u(p) = \phi'(p)$, rather than for $\phi(p)$. Using the WKB ansatz $u(p) = b(p)e^{-NS(p)}$ in the quasi-stationary equation

$$\frac{1}{3N^2}(1 + p + p^2)u'' - pu = 0,$$  \hfill (64)

we obtain

$$\frac{(1 + p + p^2)}{3N^2}[N^2(S')^2b - 2NS'b' - NS''b] - pb = 0,$$  \hfill (65)

where we have neglected the sub-subleading term proportional to $b''/N^2$. In the leading order we obtain $S'(p) = -\psi(p)$ (the solution with $S'(p) = \psi(p)$ is non-physical and must be discarded). The arbitrary constant can be fixed by putting $S(1) = 0$, and we obtain

$$S(p) = -\int_1^p \psi(x) \, dx,$$  \hfill (66)

with $\psi(x)$ from equation (63). This result can be expressed via elliptic integrals, but we will not need these cumbersome formulae.

\vspace{1cm}

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Figure 7. Branching and triple annihilation. Shown are zero-energy lines of Hamiltonian (62) on the \((p, q)\) phase plane. The thick solid line is the instanton \(q = -S'(p) = \psi(p)\), given by equation (63). Here \(q_1 = 1\), and the area of the shaded region is equal to \(S_0\) from equation (75). The dashed line denotes a non-physical orbit.

In the subleading order, equations (65) and (66) yield a first-order ordinary differential equation for \(b(p)\) whose general solution is

\[
b(p) = \frac{C(1 + p + p^2)^{1/4}}{p^{1/4}}. \tag{67}
\]

We demand \(u(1) \simeq -n_1 = -N\) (see equation (45)) and obtain the quasi-stationary WKB solution for \(u(p)\):

\[
u_{\text{WKB}}(p) = -\frac{N(1 + p + p^2)^{1/4}}{(3p)^{1/4}}e^{-NS(p)} \tag{68}
\]

with \(S(p)\) from equation (66). Now one can check that asymptote (68) is valid when \(p \gg N^{-2/3}\); otherwise it is not justified to neglect the term \(b''(p)\) in equation (65). Again, the quasi-stationarity and the WKB approximation break down in the vicinity of the point where the fast and slow WKB modes are strongly coupled. In this example this point is at \(p = 0\), whereas in the previous example it was at \(p = p_f \neq 0\). That the WKB breaks down here at \(p = 0\) is a special, non-generic situation resulting from the absence of the linear decay process \(A \rightarrow 0\) from the set of reactions \(A \rightarrow 2A\) and \(3A \rightarrow 0\) that we are dealing with.

To remedy the divergence of the WKB solution at \(p = 0\), one needs to account for a deviation from quasi-stationarity. The corresponding non-quasi-stationary solution of equation (59) is perturbative in \(E\), as in the previous example, so the equation that we need to solve is

\[
\frac{1}{3N^2}(1 - p^3)u'' + p(p - 1)u = -E. \tag{69}
\]
The corresponding homogeneous equation, equation (61), is not solvable in known special functions. Therefore, we will solve equation (69) approximately in two separate regions and match the solutions in their region of joint validity.

The first region, which we call ‘left’, is $p<0$ (and not too close to zero; see below). Here we can neglect the $u''$ term in equation (69) and obtain

$$u^{\text{left}}(p) \simeq \frac{E}{p(1-p)}. \hspace{1cm} (70)$$

This asymptote, valid when $-p \gg N^{-2/3}$, corresponds to neglecting the high order reaction $3A \rightarrow 0$ at small population sizes. As in the previous example, $u^{\text{left}}(p)$ is exponentially small. By choosing an exponentially small solution for $u(p)$ in the left region, we effectively discarded two other linearly independent solutions of equation (61) which are singular at $p = e^{2\pi i/3}$ and $e^{4\pi i/3}$. As $p_f = 0$ here, one can actually put $u = 0$ in the left region and still accurately determine the QSD (see footnote 5).

The second region is the boundary layer with $|p| \ll 1$, where equation (69) becomes

$$\frac{1}{3N^2}u'' - pu = -E, \hspace{1cm} (71)$$

The general solution of this equation is

$$u^{\text{bl}}(p) = \left[ c_1 + \alpha^2 \pi E \int_0^p \text{Bi}(\alpha s) \, ds \right] \text{Ai}(\alpha p) + \left[ c_2 - \alpha^2 \pi E \int_0^p \text{Ai}(\alpha s) \, ds \right] \text{Bi}(\alpha p), \hspace{1cm} (72)$$

where $\text{Ai}(y)$ and $\text{Bi}(y)$ are the Airy functions of the first and second kind, respectively [23], and $\alpha = (3N^2)^{1/3}$.

Now we can find the unknown constants $c_1$ and $c_2$ (assuming for a moment that $E$ is known) by matching the asymptotes (70) and (72) in their common region $N^{-2/3} \ll -p \ll 1$. As $u^{\text{left}}(p)$ is exponentially small at $N^2|p|^3 \gg 1$, the boundary layer solution $u^{\text{bl}}(p)$ from equation (72) must also be exponentially small there. Evaluating the integrals in equation (72) at $p = -\infty$ and using the identities $\int_0^\infty \text{Bi}(s) \, ds = 0$ and $\int_{-\infty}^0 \text{Ai}(s) \, ds = 2/3$, we arrive at

$$c_1 \simeq 0, \hspace{1cm} c_2 \simeq -\frac{2\pi EN^{2/3}}{3^{2/3}}. \hspace{1cm} (73)$$

Now we can find the extinction rate $E$ by matching the asymptotes of $u^{\text{WKB}}(p)$ and $u^{\text{bl}}(p)$ in their common region $N^{-2/3} \ll p \ll 1$. The $p \ll 1$ asymptote of the WKB solution (68) is

$$u^{\text{WKB}} \simeq -\frac{N}{(3p)^{1/4}}e^{-NS_0e^{(2/\sqrt{3})Np^{3/2}}}, \hspace{1cm} (74)$$

where

$$S_0 = \int_0^1 \left( \frac{3x}{1 + x + x^2} \right)^{1/2} \, dx = 0.836 \, 367 \cdots, \hspace{1cm} (75)$$

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is the shaded area in figure 7. Let us obtain the $p \gg N^{-2/3}$ asymptote of $u^{bl}(p)$ (72). First, for $z \gg 1$

$$\text{Ai}(z) \simeq \frac{e^{-(2/3)z^{3/2}}}{2\pi^{1/2}z^{1/4}}, \quad \text{Bi}(z) \simeq \frac{e^{(2/3)z^{3/2}}}{\pi^{1/2}z^{1/4}}. \quad (76)$$

Now we need to evaluate the integrals in equation (72). As we are interested in the region of $N^2p^3 \gg 1$, the integral of $\text{Ai}(\alpha s)$ can be evaluated by putting $p = \infty$ and using the saddle point approximation, arriving at

$$\int_{0}^{\infty} \text{Ai}[(3N^2)^{1/3}s] ds = \frac{1}{3^{4/3}N^{2/3}}. \quad (74)$$

The main contribution to the integral of $\text{Bi}(\alpha s)$ at $N^2p^3 \gg 1$ comes from the vicinity of $s = p$, where $\text{Bi}(\alpha s)$ is exponentially large; see equation (76). Expanding the exponent in a Taylor series around $s = p$, we obtain in the leading order

$$\int_{0}^{p} \text{Bi}[(3N^2)^{1/3}s] ds \simeq \frac{e^{(2/\sqrt{3})Np^{3/2}}}{3^{7/12}2^{1/2}N^{7/6}p^{3/4}}. \quad (77)$$

Now one can see from equation (73) that the main contribution to $u^{bl}(p)$ (72) comes from the $\text{Bi}(\alpha p)$ term, and we obtain

$$u^{bl} \simeq -\frac{3^{1/4}\sqrt{\pi NE}}{p^{1/4}}e^{(2/\sqrt{3})Np^{3/2}}. \quad (77)$$

Matching equations (74) and (77), we obtain

$$E = \sqrt{\frac{N}{3\pi}}e^{-NS_0}. \quad (78)$$

The MTE in physical units is given by $\tau_{\text{ex}} = (\lambda E)^{-1}$, which is exponentially large in $N$, as expected. A comparison between the analytical result for the extinction rate (78) and a numerical result, obtained by solving (a truncated version of) master equation (57), is shown in figure 8. For $N \gg 1$ the agreement is excellent.

Now let us calculate the QSD. Combining equation (4) with equations (33) and (34), we obtain

$$\pi_{n \geq 1} = -\frac{1}{2\pi ni} \int \frac{u(p)}{p^n} dp. \quad (79)$$

For $n \gg 1$ we can use the WKB asymptote (68):

$$\pi_{n \gg 1} \simeq -\frac{1}{2\pi ni} \int \frac{u^{\text{WKB}}(p)}{p^n} dp = \frac{N}{2\pi ni} \int \frac{1 + p + p^2}{(3p)^{1/4}} \exp[N \int_{1}^{p} \psi(x) dx] \frac{dp}{p^n}, \quad (80)$$

with $\psi(x)$ given by equation (63). As $N \gg 1$ and $n \gg 1$, this integral can be evaluated via saddle point approximation [24]. Let us define $f(p) = N \int_{1}^{p} \psi(x) dx - n \ln p$. The saddle point equation $f'(p_*) = 0$ reduces to a cubic equation

$$\frac{3p^3}{1 + p + p^2} = \left(\frac{n}{N}\right)^2, \quad (81)$$

$$\text{doi:10.1088/1742-5468/2010/07/P07018} \quad 23$$
Figure 8. Branching and triple annihilation. Shown is a comparison between the extinction rate (78) (solid line) and the extinction rate $-\ln(1 - P_0^n(t))/t$ (crosses) found from a numerical solution of the master equation (57) at different values of $N$. The inset shows the ratio of the two rates.

which has one and only one real root $p_* = p_*(n/N)$. As $f''(p_*) > 0$, we must choose a contour in the complex $p$ plane which goes through this root perpendicularly to the real axis. The Gaussian integration yields

$$
\pi_n \approx \frac{N(1 + p_* + p_*^2)^{1/4}}{n\sqrt{2\pi f''(p_*) (3p_*)^{1/4}}} \exp\left[\frac{\int_{p_*}^{P} \psi(x) \, dx}{p_*^2}\right];
$$

we omit a cumbersome expression for $f''(p)$. Note, that for $n \gg 1$, the saddle point $p_*$ is always obtained in the region where $u^{WKB}(p)$ is valid; see below. Let us calculate the $1 \ll n \ll N$ and $n \gg N$ asymptotes of equation (82) with exponential accuracy, $\ln \pi_n \approx f(p_*)$. For $n \ll N$ the saddle point, given by equation (81), is obtained at $p_* = [n/(\sqrt{3}N)]^{2/3} \ll 1$. Here it suffices, in the leading order in $n/N$, to put $p_* = 0$ in the upper bound of the integral in equation (66). Then the integral yields $S_0$ from equation (75). For $n \gg N$ we obtain $p_* = [n/(\sqrt{3}N)]^2 \gg 1$. Here a dominant contribution to the integral in equation (66) comes from the region of $p_* \gg 1$ which enables one to simplify the integrand. The resulting asymptotes are

$$
\ln \pi_n \approx \begin{cases} N \left[ -S_0 + 2n \ln N - \ln n \right] + O\left(\frac{n}{N}\right), & n \ll N \\ \frac{2n}{N} \ln \frac{n}{N} - 1 - \ln \sqrt{3} + O(1), & n \gg N. \end{cases}
$$

Notice that each of these tails of the QSD are non-Gaussian. The $n \gg N$ tail decays faster than exponentially, thus justifying a posteriori our assumption that $\phi(p)$ is an entire function in the complex $p$ plane.

At $|n - N| \ll N$, the saddle point, given by equation (81), is obtained at $p_* = 1 + (n - N)/N$, and we arrive at a Gaussian asymptote

$$
\pi_n \approx \frac{1}{\sqrt{2\pi N}} e^{-(n-N)/(2N)};
$$
the pre-exponent is fixed by normalization. Equation (84) holds for $|n - N| \ll N^{2/3}$; this condition is tighter than $|n - N| \ll N$. Note, that the Gaussian asymptote of the QSD can also be found by directly calculating the mean and variance of the distribution. These (and other higher cumulants of the distribution) can be found by using derivatives of $G(p, t)$ with respect to $p$ at $p = 1$; see equation (2). Indeed, from equations (2) and (6), the mean of the QSD (at times $t_r \ll t \ll \tau_{ex}$) is given by $\bar{n} = \partial_p G|_{p=1} \simeq -u(p = 1) = N$, where here we have used $u = u^{WKB}(p)$ given by equation (68). In its turn the variance in the leading order is

$$V = \bar{n}^2 - \bar{n}^2 = \sum_{n=0}^{\infty} n^2 P_n(t) - \left( \sum_{n=0}^{\infty} n P_n(t) \right)^2 = [\partial_{pp} G + \partial_p G - (\partial_p G)^2]|_{p=1}
\simeq -u'(1) - u(1) - [u(1)]^2 \simeq N,$$

recovering the Gaussian asymptote (84).

At $n = O(1)$ the QSD can be evaluated directly from

$$\pi_n = \frac{1}{n!} \left. \frac{d^{n-1} u(p)}{dp^{n-1}} \right|_{p=0}, \quad n \geq 1.
$$

Here one should use the boundary layer solution around $p = 0$, given by equations (72) and (73). This yields

$$\pi_1 = \frac{\Gamma(1/3)EN^{2/3}}{3^{1/3}}, \quad \pi_2 = \frac{\pi E N^{4/3}}{3^{1/6} \Gamma(1/3)}, \quad \text{and} \quad \pi_3 = \frac{EN^2}{2}. \quad (85)$$

To calculate other $n = O(1)$ terms, one can use a recursion relation obtainable from the master equation (57) with $\dot{P}_n = 0$. Indeed, at $n \ll N$ one can neglect the terms $n(n-1)(n-2)P_n$ and $(n-1)P_{n-1}$ compared with the terms $(n+3)(n+2)(n+1)P_{n+3}$ and $nP_n$, respectively, and arrive at the following relation:

$$\pi_{n+3} = \frac{3N^2 n}{(n+3)(n+2)(n+1)} \pi_n. \quad (86)$$

Note, that the small-$n$ (86) and the WKB (82) segments of the QSD have a region of joint validity at $1 \ll n \ll N$.

A comparison between the WKB result (82) and a numerical solution of (a truncated version of) master equation (57) is shown in figure 9. The inset compares the $n \ll N$ analytical asymptote (see equations (85) and (86)) with numerical results. Excellent agreement is observed in both cases. It can be also seen that the Gaussian approximation (84) strongly overestimates the QSD in the region of low $n$, and underestimates it in the region of high $n$.

5. Discussion

The $p$-space representation provides a unique perspective on the theory of large fluctuations in populations undergoing Markovian stochastic gain–loss processes. The stationary distribution of the population size is encoded in the ground-state eigenfunction of a Sturm–Liouville (spectral) problem for the probability generating function. In the case
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Figure 9. Branching and triple annihilation. Shown is the natural logarithm of the QSD versus $n$ for $N = 20$. The dashed line is WKB solution (82), the dash–dotted line is the Gaussian approximation (84), and the solid line is the numerical solution of the (truncated) master equation (57). Inset: the $n \ll N$ asymptote of the QSD obtained analytically (equations (85) and (86)) ($\times$s) and numerically (fat dots).

of a long-lived metastable population on the way to extinction, the MTE and the quasi-stationary distribution of population size are encoded in the eigenfunction of the lowest excited state. The uniqueness of solution in these problems is guaranteed by the condition that the probability generating function is an entire function on the whole complex $p$ plane except at infinity. As this work has demonstrated (see also [16,19,20,22,25,27]), the $p$-space representation in conjunction with the WKB approximation and other perturbation tools employing a large parameter $N \gg 1$ (the mean population size in the stationary or metastable state) yields accurate results for extreme statistics for a broad class of problems of stochastic population dynamics. Such accuracy is usually impossible to attain via the van Kampen system size expansion which approximates the exact master equation by a Fokker–Planck equation.

How does the $p$-space approach compare with the ‘real-space’ WKB method of [5,6,15,17,18] when the stationary or metastable population size is large, $N \gg 1$? One advantage of the $p$-space representation is that, for two-body reactions, there is no need for the WKB approximation, as the quasi-stationary equation in this case is always solvable exactly. Another advantage appears when the WKB solution for $G(p,t)$ is valid for every $p \gtrsim 0$, as occurs in the molecular hydrogen production problem (section 3). In such cases one directly finds the entire probability distribution function, including the region of small $n = \mathcal{O}(1)$. In the real-space approach a separate (non-WKB) treatment of the $n = \mathcal{O}(1)$ region and a matching with the WKB solution valid at $n \gg 1$ would be needed [18].

Still, in our experience, every problem which includes the large parameter $N \gg 1$, and can be solved in the $p$ space, can also be solved in the ‘real’ space. Furthermore, for populations exhibiting escape to infinity [5], escape to another metastable state [17], or
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Scenario B of extinction [18], the \( p \)-space representation encounters significant difficulties. One difficulty is that one should account for a constant-current WKB solution in these cases [5, 17, 18]. The constant-current solution comes from the deterministic line \( p = 1 \) of the phase plane of the underlying classical Hamiltonian. In the \( p \) representation this line is vertical, as in figures 1, 5 and 7, and so the constant-current solution cannot be easily accounted for. In addition, it is unclear how to deal with the region of non-uniqueness of \( q = q(p) \) which is inherent, in the \( p \) representation, in these cases. There are two WKB solutions in this region, one of them exponentially small compared with the other. The real-space approach avoids these difficulties, and the solution in these cases can be worked out in a straightforward manner [5, 17, 18].

An important advantage of the \( p \)-space representation stems from the fact that the evolution equation for \( G(p, t) \) is exactly equivalent to the original master equation. Therefore, the \( p \)-space approach is especially valuable for exact analysis, as illustrated by the example of molecular hydrogen production; see [8] and section 3.

Finally, generalization of the \( p \) representation to interacting multi-species populations is quite straightforward; see [28]. The resulting multi-dimensional evolution equation for the probability generating function can be analyzed using the WKB approximation. At present only the leading order WKB approximation for population extinction is available, and this is regardless of whether one uses the \( p \)-space or \( n \)-space approach. In the leading WKB order the problem again reduces to finding a nontrivial zero-energy trajectory of the corresponding classical Hamiltonian, and the action along this special trajectory. This problem can be solved numerically. If additional small parameters are present, the problem may become solvable analytically, again in both \( p \) and \( n \) spaces [28]–[30].

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