Non-conserving zero-range processes with extensive rates under resetting

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Abstract
We consider a non-conserving zero-range process with hopping rate proportional to the number of particles at each site. Particles are added to the system with a site-dependent creation rate, and vanish with a uniform annihilation rate. On a fully-connected lattice with a large number of sites, the mean-field geometry leads to a negative binomial law for the number of particles at each site, with parameters depending on the hopping, creation and annihilation rates. This model can be mapped to population dynamics (if the creation rates are reproductive fitnesses in a haploid population, and the hopping rate is the mutation rate). It can also be mapped to a Bianconi–Barabási model of a growing network with random rewiring of links (if creation rates are the rates of acquisition of links by nodes, and the hopping rate is the rewiring rate). The steady state has recently been worked out and gives rise to occupation numbers that reproduce Kingman's house-of-cards model of selection and mutation. In this paper we solve the master equation using a functional method, which yields integral equations satisfied by the occupation numbers. The occupation numbers are shown to forget initial conditions at an exponential rate that decreases linearly with the fitness level. Moreover, they can be computed exactly in the Laplace domain, which allows to obtain the steady state of the system under resetting. The result modifies the house-of-cards result by simply adding a skewed version of the initial conditions, and by adding the resetting rate to the hopping rate.

1. Introduction
Non-conserving systems of particles on a fully connected lattice are useful models to describe out-of-equilibrium systems with varying levels of fitness. In the context of population dynamics, particles represent individuals in a haploid population, and fitness is understood as reproductive fitness. In the context of network science, particles at a node represent links to this node (this mapping from configurations of links to configurations of particles was used in the construction of the Bianconi–Barabási model of a growing network [1]), and fitness is understood as the ability to acquire new links.

The accumulation of particles at sites of higher fitness results from a selection process. This effect can be attenuated by other processes: vanishing of particles, and production of particles of random fitness. This production process corresponds to mutation in a population (and it corresponds to random rewiring of links in a network). One may ask whether a finite proportion of the particles can condense at the highest fitness level, provided death and mutation rates are low enough. In [2], such a model of particles on a lattice was mapped to a non-conserving zero-range-process (ZRP) [3–6] with extensive hopping rates, describing the occupation number of each fitness level. The zero-range process is well-known to give rise to condensation, whose emergence and dynamics are well studied in the case of decreasing hopping rates [7–14]. Non-conserving ZRPs coupled to reservoirs through open boundaries are studied in [15], and stationary currents can be induced by asymmetry of the hopping rate at a defect [16].

The steady state of the non-conserving ZRP was worked out in [2] from a master equation by adapting techniques from [17, 18]. The expectation value of the occupation number of each fitness level in the steady state...
is the sum of two terms: a skewed version of the mutant density, and a term that approaches an atom supported at maximum fitness in a certain regime of low death and mutation rates. These two terms evoke the result of the deterministic measure-valued house-of-cards model introduced by Kingman in population dynamics to describe the balance of selection and mutation [19] (which assumes non-overlapping generations and large populations). As the steady state of the system is unique, the occupation numbers forget the initial conditions. However, the rate at which they do so may depend on the fitness.

On the other hand, a system may be put in contact with initial conditions at random times by undergoing stochastic resetting. This process resets the system to its initial configuration or to an ensemble of resetting configurations [20, 21], and keeps it from its stationary state. The system under resetting can feature a non-equilibrium stationary state, depending on the parameters of the resetting process [22]. Characterisation of such a non-equilibrium stationary state has recently become a major focus of activity in statistical physics [23–25]. The field enjoys a broad range of applications including RNA polymerisation processes [26, 27], active matter [28–30] and randomised searching problems [31] (see the review [32] and references therein).

Moreover, the probability law of configurations of a system under resetting is related to the probability law of the ordinary system (without resetting) by an integral equation, obtained from a renewal argument [20, 29, 33–36]. In particular, the probability law at steady state of the system under resetting can be worked out from the Laplace transform of the probability law at steady state of the ordinary system. In the present model of particles, a resetting event corresponds to a massive extinction of population or to a destruction of links in the network, restoring the system to its initial configuration.

In this paper we characterise the behaviour of a non-conserving ZRP at finite time (in particular, we work out how fast the occupation numbers forget the initial conditions), in order to characterise the steady state of the system under resetting. In section 2 we review the model and introduce notations, recalling the interpretations of the parameters in population dynamics and network science. In section 3 we introduce the generating function of the model and work out the PDE it satisfies, based on the master equation. This PDE is non-linear, because of the presence of the average density of the system as a coefficient. This situation occurs in balls-in-boxes models, such as the backgammon model [7, 37–39] (in which a fixed number of balls are distributed among boxes, and the energy of a configuration is given by the number of empty boxes). In section 4 we adapt the functional approach taken in [40] to solve the master equation: the moment-generating function is considered as a functional of the density, which allows to solve the PDE after a change of variables. A consistency condition is imposed, which yields an integral equation satisfied by the density. This equation is solved in the Laplace domain. In section 5, this solution is used to work out the expectation values of the occupation numbers at each fitness level of the system undergoing stochastic resetting to its initial configuration at a fixed rate.

2. Review of the non-conserving ZRP with extensive rates

2.1. Description of the system and quantities of interest

Consider a fully connected lattice with a large number of nodes (or states). Each of these states can be occupied by a certain number of particles. Moreover, each state carries a certain value, called its fitness level. This value is interpreted either in the sense of reproductive fitness (cell division rate) in a haploid population, or in the sense of the rate of acquisition of new links by the node in a network (see table 1 for a summary of the parameters with their interpretations).

The occupation number of each state is a random quantity, evolving through the following processes:

1. hopping to another uniformly drawn state (the particles are independent random walkers on the fully connected set of states in the system),
2. annihilation (at a uniform rate),
3. creation (at a rate that increases with the fitness level).

The above three processes were already considered in [2]. In this paper we will moreover consider stochastic resetting of the system to an empty configuration: massive extinctions occur at random times. When a massive extinction happens, all particles are instantaneously annihilated (the set of states stays fixed).

The main quantities of interest are the occupation numbers of each fitness level (the sums of the occupation numbers of the states at this fitness level). The fitness is assumed to be bounded, with a maximum of 1, as in the house-of-cards model [19]. We are going to review the formulation of the model with a discrete set of regularly-spaced fitness levels in the interval [0, 1]. In the large-\(L\) limit, the hopping process will be described in terms of the average density of the system using a mean-field approach, and the fitness levels will approach a
### Table 1. Table of notations and interpretations for the parameters of the model, in the limit of a continuum of fitness levels.

| Symbol | Values | Particles | Network | Population |
|--------|--------|-----------|---------|------------|
| $l$    | $l \in [0, 1]$ | Rate of production of particles | Rate of acquisition of links (fitness of a node in a network) | Rate of cell division in a haploid population (reproductive fitness) |
| $q$    | probability density on $[0, 1]$, satisfying $q(1) = 0$ | Density of states | Density of states | Mutant fitness |
| $n(l)$ | random integer | Total occupation number in states at level $l$ | Total number of links to nodes at level $l$ | Total population of fitness $l$ |
| $\delta$ | $\delta > 0$ | Vanishing rate | Rate of disappearance of links | Death rate |
| $\beta$ | $\beta > 0$ | Hopping rate | Rewiring rate | Mutation rate |
continuum. The evolution of the probability law of the occupation number of a given fitness level will result in the master equation (equation (13)) derived in [2], which is valid between massive extinctions.

2.2. Master equation
Let us consider a large number $L$ of regularly spaced fitness levels in the interval $[0,1]$. Let us denote by $v_k$ the number of states at fitness level $k/L$ (for each $k$ in $[1..L]$), with

$$v_k = \max\left(\left\{ \frac{1}{L} q\left(\frac{k}{L}\right) V , 1 \right\} \right) = \frac{1}{L} q\left(\frac{k}{L}\right) V + \zeta_k,$$

(1)

where $V$ denotes a large integer, satisfying $V \gg L$. The symbol $q$ denotes a fixed probability density, defined on the continuum $[0,1]$, one of the parameters of the model (which corresponds to the mutant density in Kingman’s house-of-card model of population dynamics [19]). Let us assume that the density $q$ vanishes at maximum fitness:

$$q(1) = 0,$$

(2)

so that there is only one state at the maximum fitness level. Square brackets denote the integer part, and $\zeta_k$ is a number in $[-1,1]$.

The total number of states in the system is of order $V$ (it is not exactly equal to $V$ due to the integer-part prescription used in equation (1) to obtain integer numbers from the density $q$):

$$\sum_{k=1}^{L} v_k = \left(\frac{1}{L} \sum_{k=1}^{L} q\left(\frac{k}{L}\right) + \frac{1}{V} \sum_{k=1}^{L} \zeta_k \right) V.$$

(3)

As $|\zeta_k| < 1$, the absolute value of the second sum is lower than $L/V$.

For each integer $k$ in $[1..L]$, let us label the $v_k$ states with fitness $k/L$ by integers in $[1..v_k]$, and denote by $\nu(k,s)$ the occupation number of the state labelled by $s$. The total number $n_k$ of particles at fitness level $k/L$ is expressed as

$$n_k = \sum_{s=1}^{v_k} \nu(k,s).$$

(4)

Let us describe the hopping process, to review how it induces a ZRP with extensive rates between fitness levels. The particles are independent random walkers on the fully connected set of states described by equation (1). Each of these walkers hops at a fixed rate $\beta$ to a uniformly drawn target state. Consider the hopping processes that increase the occupation number of the set of states at a fixed level of fitness $m/L$, for some integer $m$ in $[1..L]$. Let us express the total rate of these processes, using equations (1), (3) and (4):

$$\beta \sum_{k=m}^{L} \sum_{s=1}^{v_k} \nu(k,s) \frac{L}{\sum_{j=1}^{v_j} L v_j} = \beta \left(\sum_{m=k}^{L} n_k\right) \frac{1}{\sum_{j=1}^{L} q\left(\frac{m}{L}\right) + \frac{\zeta_m}{V}}$$

$$= \beta \left(\sum_{m=k}^{L} n_k\right) \frac{1}{\sum_{j=1}^{L} q\left(\frac{m}{L}\right) + \frac{1}{\sum_{j=1}^{L} \zeta_j}}$$

$$= \beta \left(\sum_{m=k}^{L} n_k\right) \frac{1}{\sum_{j=1}^{L} q\left(\frac{m}{L}\right) + \frac{1}{\sum_{j=1}^{L} \zeta_j}}$$

$$= \beta \left(\frac{1}{L} \sum_{k=1}^{L} n_k \frac{n_m}{L} \right) \frac{1}{\sum_{j=1}^{L} q\left(\frac{m}{L}\right) + \frac{1}{\sum_{j=1}^{L} \zeta_j}}$$

$$\rightarrow \beta \left(\frac{1}{L} \sum_{k=1}^{L} n_k \frac{n_m}{L} \right) \frac{q\left(\frac{m}{L}\right)}{\sum_{j=1}^{L} q\left(\frac{m}{L}\right) + \frac{1}{\sum_{j=1}^{L} \zeta_j}}$$

(5)

At fixed $L$, for a given configuration of occupation numbers, we can define a function $n^{(L)}$ on the interval $[0,1]$ by

$$l \in [0,1] \mapsto n^{(L)}(l) = n_{[0,l]}.$$

(6)

which is piecewise constant. In the large-$L$ limit, let us denote the limit of $n^{(L)}(l)$ by $n(l)$. Repeating this procedure for all configurations of occupation numbers induces a continuous one-parameter family of random variables, the random occupation numbers of fitness levels. Let us denote by $p_l(n,t)$ the probability law of $n(l)$ at time $t$:

$$\forall l \in [0,1], \quad p_l(n,t) = P(n(l) = n \text{ at time } t).$$

(7)
The average density defined of the system can therefore be expressed in the large-\(L\) limit as an integral:

\[
\bar{\eta}(t) = \sum_{n \geq 0} n \rho_p(n, t), \quad \rho(t) = \int_0^1 \bar{\eta}(t) \, dl.
\] (8)

Moreover, the denominator in equation (5) is a Riemann sum which goes to 1 when \(L\) goes to infinity, because \(q\) is a probability density. In the continuum limit, we consider a fixed value of the fitness \(l\) in [0,1], and in the rate of hopping processes to states with fitness \(m/L\), we take the limit in which both integers \(L\) and \(m\) go to infinity, while the ratio \(m/L\) goes to \(l\). Moreover, in the large-\(L\) limit, each fitness level is connected by the hopping process to a large number of other fitness levels. In this limit, we are therefore in a situation that is suitable for a mean-field approximation, as in the dynamics of urn models [6, 10, 41]. We therefore approximate the factor \((\sum_{n=1}^l v_k) / L - n_m / L\) by the average density \(\rho\). Neglecting the term \(n_m / L\) (which depends on the destination level) corresponds to the fact that hopping processes relate states with distinct fitness levels with a probability that goes to one when \(L\) goes to infinity.

Similarly, let us express the total rate of the hopping processes that decrease the occupation number of the \(n\)th of the set of states of fitness \(m/L\):

\[
\beta \sum_{k=1}^m \sum_{j=1}^l \nu(m, s) \frac{v_k}{\sum_{j=1}^l v_j} = \beta n_m \frac{\sum_{k=1}^m v_k}{\sum_{j=1}^l v_j} = \beta n_m \left(1 - \frac{v_m}{\sum_{j=1}^l v_j}\right) \left(1 - \frac{1}{\frac{1}{L} \sum_{j=1}^l v_j}\right).\] (9)

The factor of \(n_m\) is the only dependence of this rate on the occupation numbers, which is the defining property of the ZRP. Taking again the limit of large \(L\) and \(m\), with \(m/L = l\) fixed, the last factor in the above expression goes to 1. The total rate of the hopping process from the states at level \(l\) therefore goes to \(\beta n(l)\).

We can therefore combine the continuum limit of equations (5) and (9), to express the contribution of the hopping process to the master equation for the occupation number at fitness level \(l\):

\[
\forall n \in \mathbb{N}, \quad \left(\frac{dp_l(n, t)}{dt}\right)_{\text{hopping}} = \beta \rho(t) q(l) p_l(n-1, t) \theta(n) - \beta \rho(t) q(l) p_l(n, t) - \beta \rho p_l(n, t) \theta(n) + \beta (n+1) p_l(n+1, t),
\] (10)

where the first two terms account for hopping processes to level \(l\) (one increasing the occupation number from \(n - 1\) to \(n\), with the step-function factor \(\theta(n) = 1(n > 0)\) ensuring that this term exists only for \(n > 0\), the other increasing the occupation number from \(n\) to \(n + 1\)). The last two terms account for hopping processes from level \(l\) (the third term decreases the occupation number from \(n\) to \(n - 1\), again with a factor \(\theta(n)\) even though it is redundant due to the factor of \(n\), and the fourth term decreases the occupation number from \(n + 1\) to \(n\)). The assumption of equation (2) implies that the occupation level of the maximum fitness level is never increased by the hopping process. Moreover, the factor of \(q(l)\) in the first two terms yields the interpretation of the density \(q\) in population dynamics as the mutant density [2, 19]: when a new mutant is added to the population, its fitness is drawn from the probability distribution \(q\). An accumulation of a large fraction of the total population at maximum fitness could therefore only be attributed to selection, and not to beneficial mutations. The prescription of equation (1) ensures that the density of states goes to the fixed density \(q\) in the limit of a large number of nodes and a large number of fitness levels (it is not the only prescription with such a limit: there needs to be a non-zero number of states of maximum fitness to support particles, but any fixed number independent of \(L\) and \(V\) would do).

Let us describe the annihilation and creation processes directly in the continuum limit, as they do not couple occupation numbers of distinct fitness levels. All particles in the system are assumed to be annihilated at the same rate, denoted by \(\delta\). The total annihilation rate at a fixed fitness level \(l\) is therefore proportional to the occupation number of this level. The annihilation process induces the following two terms in the master equation:

\[
\forall n \in \mathbb{N}, \quad \left(\frac{dp_l(n, t)}{dt}\right)_{\text{annihilation}} = - \delta n p_l(n, t) \theta(n) + \delta (n+1) p_l(n+1, t),
\] (11)

where the first term corresponds to decreasing the occupation number from \(n\) to \(n - 1\), with the constraint \(n > 0\), and the second term corresponds to decreasing the occupation number from \(n + 1\) to \(n\).

The rates of the creation process are biased by the fitness level: we consider the rate of creation of particles at level \(l\) to be \(h(n(l)) + 1\). The factor \(l\) models the selection process: rates of creation increase with fitness. The other factor is the occupation number of the fitness level after the creation of a new particle. This amounts to modelling the creation process as an annihilation process reversed in time. In the population-dynamics
interpretation this implies that there is a spontaneous generation of particles at empty fitness levels (an operator adds an individual at fitness level \( l \) if this level becomes empty, to keep the selection process going). In the network interpretation of the model, this is quite natural as nodes can acquire links from other nodes even if they do not have any yet. The creation process therefore induces the following two terms in the master equation:

\[
\forall n \in \mathbb{N}, \quad \left( \frac{dp_l(n, t)}{dt} \right)_{\text{creation}} = \ln p_l(n - 1, t) \theta(n) - l(n + 1) p_l(n, t),
\]

where the first term corresponds to increasing the occupation number from \( n - 1 \) to \( n \), with the constraint \( n > 0 \), and the second term corresponds to increasing the occupation number from \( n \) to \( n + 1 \). Setting the maximum level of fitness to 1 is equivalent to setting the time scale of the process: starting from a configuration with no particles, the rate of creation of particles at the highest fitness level equals 1.

If we disregard the resetting of the occupation numbers to 0 induced by massive extinctions, or alternatively consider the evolution of the system between resetting times, the probability law of the occupation number of fitness level \( l \) satisfies the following master equation [2], induced by the hopping, annihilation and creation processes (parametrised by the quantities listed in table 1):

\[
\frac{dp_l(n, t)}{dt} = \theta(n) \left\{ (\beta \rho(t) q(l) + \ln) p_l(n - 1, t) - (\delta + \beta) n p_l(n, t) \right\}
+ (\delta + \beta) (n + 1) p_l(n + 1, t) - (\beta \rho(t) q(l) + l(n + 1) p_l(n, t), \quad \forall n \geq 0.
\]

At steady state (in the absence of resetting events) the probability distribution of particles at each fitness level is negative binomial. This was established in [2] by putting the l.h.s of equation (13) to zero. An expression for the steady-state occupation numbers \( \pi_l(\infty) \) was derived. It consists of two terms: a skewed version of the measure \( q \), and a term that gives rise to an atom at maximum fitness when the sum of vanishing and hopping rates \( \delta + \beta \) decreases to 1:

\[
\pi_l(\infty) = \frac{1}{\beta + \delta - 1} + \frac{\beta \rho(\infty) q(l)}{\beta + \delta - 1},
\]

\[
\rho(\infty) = \int_0^1 \frac{1}{\delta + \beta - 1} dl \left( 1 - \beta \int_0^1 \frac{q(l) dl}{\delta + \beta - 1} \right)^{-1},
\]

provided \( \delta + \beta > 1 \) and \( \beta < \beta_c = \left( \int_0^1 \frac{q(l) dl}{\delta + \beta - 1} \right)^{-1}. \)

The structure of this expression, together with the critical value of the hopping rate, is very reminiscent of the steady state of the house-of-cards model [19]. The steady state is unique and does not depend on the initial conditions \( (\pi_l(0))_{l \in [0,1]} \). In the rest of the paper we will assume that the rates \( \delta \) and \( \beta \) satisfy the conditions of equation (16) leading to a steady state. We are going to study the master equation at finite time in order to work out how fast each fitness level forgets initial conditions, in the absence of resetting events. The solution will be used to address resetting events in section 5.

3. From the master equation to the generating function

Let us introduce the generating function, which characterises the probability law of all the configurations of occupation numbers:

\[
H(J, l, t) := \sum_{n \geq 0} p_l(n, t) J^n.
\]

In particular, the average occupation numbers and the density parameter can be expressed at time \( t \) in terms of \( H \) as follows:

\[
\pi_l(t) = \frac{\partial H}{\partial J} \bigg|_{J=1} (J, l, t), \quad \rho(t) = \int_0^1 \left( \frac{\partial H}{\partial J} \right)_{J=1} (J, l, t) dl.
\]

The master equation induces a PDE in variables \( t \) and \( J \), satisfied by the generating function at each level \( l \). Let us write it with the terms in the same order as in equation (13):
Because of the dependence of the coefficients on the density $\rho$ (defined in terms of the probability laws of occupation numbers in equation (18)), the PDE is non-linear:

$$\frac{\partial H}{\partial t} = (1 - J) \left( (-1 - \beta \rho q(l)) H + (1 + \zeta - lj) \frac{\partial H}{\partial l} \right), \tag{20}$$

where

$$\beta + \delta = 1 + \zeta, \tag{21}$$

with $\zeta > 0$ (this assumption, equation (16) ensures that the sum of the vanishing and hopping rates is high enough to prevent an exponential divergence of the occupation number at maximum fitness). The non-linearity can be addressed using the functional method (see [40] for an application of this method to the backgammon model). We are going to consider the generating function as a functional of the density $\rho(t)$, and to impose a closure condition through the general definition (equation (18)) of the density.

4. The generating function as a functional of the density

4.1. Change of variables

To work out the functional dependence of the generating function on the density, let us look for a change of variables that would transform equation (20) into an ordinary differential equation in the time variable. The equation contains no derivative w.r.t. the fitness variable $l$, so we denote the new variables by $(v, l, t)$ and look for a function $J(v, l, t)$, so that the generating function can be expressed in the new variables as:

$$\hat{H}(v, l, t) := H(J(v, l, t), l, t). \tag{22}$$

Taking the derivative of equation (22) w.r.t. time we obtain:

$$\frac{\partial \hat{H}(v, l, t)}{\partial t} = \frac{\partial H(J(v, l, t), l, t)}{\partial J} \frac{\partial J(v, l, t)}{\partial t} + \frac{\partial H(J(v, l, t), l, t)}{\partial t}. \tag{23}$$

Inspecting equation (20), we impose the following condition, in order to match the derivatives of the moment-generating function w.r.t. $J$:

$$\frac{\partial J}{\partial t} = (J - 1)(1 + \zeta - lj). \tag{24}$$

As the parameter $\rho$ is a function of time only, and the density $q$ is a function of $l$ only, equation (20) can be rewritten in the variables $(v, l, t)$ as

$$\frac{\partial \hat{H}(v, l, t)}{\partial t} = (1 - J(v, l, t))(-1 - \beta \rho(t)q(l))\hat{H}(v, l, t). \tag{25}$$

We have to integrate equation (24) w.r.t. time to work out the change of variables. The inverse of the r.h.s. is a rational function of the parameter $J$, with two poles, at $J = 1$ and $J = (1 + \zeta)/l > 1$, for any fixed $l$ in $[0,1]$. Decomposing it into simple elements yields:

$$\frac{1}{(J - 1)(1 + \zeta - lj)} = \frac{1}{1 + \zeta - l} \left( \frac{1}{J - 1} - \frac{l}{lj - 1 - \zeta} \right). \tag{26}$$

For our purposes $J$ is in the interval $[0, 1]$. The quantity $lj - 1 - \zeta$ is therefore negative, and we can rewrite equation (24) as

$$\frac{1}{1 + \zeta - l} \left( \frac{\partial \log(1 - J)}{\partial t} - \frac{\partial \log(1 + \zeta - lj)}{\partial t} \right) = 1. \tag{27}$$

Let us integrate this relation w.r.t. time and denote by $\nu$ the integration constant

$$\log \left( \frac{1 + \zeta - lj(v, l, t)}{1 - J(v, l, t)} \right) = \nu + (l - 1 - \zeta)t. \tag{28}$$
The change of variables from \((l, t)\) to \((v, l, t)\) is therefore defined by the relation:

\[
1 + \zeta - J(v, l, t) = e^{vl - 1 - \zeta t}.
\] (29)

We can express the factor of \((1 - J)\) needed in equation (25) in the variables \((v, l, t)\) as:

\[
1 - J(v, l, t) = \frac{l - 1 - \zeta}{l - e^{vl - 1 - \zeta t}},
\] (30)

which finally yields an explicit form in terms of the variables \((v, l, t)\) for the time-evolution of the generating function:

\[
\frac{1}{\tilde{H}(v, l, t)} \frac{\partial \tilde{H}(v, l, t)}{\partial t} = \frac{l - 1 - \zeta}{l - e^{vl - 1 - \zeta t}} (-l - \beta \rho(t) q(l)).
\] (31)

Integrating w.r.t. time yields an expression of the generating function as a functional of the density:

\[
\log \left( \frac{\tilde{H}(v, l, t)}{\tilde{H}(v, l, 0)} \right) = (l - 1 - \zeta) \int_{0}^{t} \frac{-l - \beta \rho(s) q(l)}{l - e^{vl - 1 - \zeta s}} ds.
\] (32)

We have to transform back to the variables \((l, t)\). Let us rewrite the functional relation (equation (22)), and the explicit change of variables equation (30), at time 0:

\[
\hat{H}(v, l, t = 0) = H(J(v, l, 0), l, 0),
\] (33)

\[
1 - J(v, l, 0) = \frac{l - 1 - \zeta}{l - e^{vl}}.
\] (34)

From the change of variables at time \(t\) (equation (30)) we have an expression of \(e^{vl}\) in terms of the quantities \(J(v, l, t), l\) and \(t\), from which we find

\[
J(v, l, 0) = 1 - \frac{l - 1 - \zeta}{l - (1 + \frac{1 + \zeta - l}{1 - J(v, l, t)}) e^{vl - \zeta t}}.
\] (35)

Going back to equation (32), we obtain the desired equation in the variables \((l, t)\):

\[
\log \left( H(J, l, t) \left( 1 - \frac{(1 - J)(l - 1 - \zeta)}{l(1 - J) - (l(1 - J) + (1 + \zeta - l)) e^{vl - 1 - \zeta t}, l, 0} \right)^{-1} \right)
\]

\[
= (l - 1 - \zeta) \int_{0}^{t} \frac{-l - \beta \rho(s) q(l)}{l - e^{vl - 1 - \zeta s}} ds
\]

\[
= (l - 1 - \zeta)(1 - J) \int_{0}^{t} \frac{-l - \beta \rho(s) q(l)}{l(1 - J) - (1 + \zeta - l)} e^{vl - \zeta t} ds
\] (36)

hence

\[
H(J, l, t) = H \left( 1 - \frac{(1 - J)(l - 1 - \zeta)}{l(1 - J) - (l(1 - J) + (1 + \zeta - l)) e^{vl - 1 - \zeta t}, l, 0} \right) \times \exp((l - 1 - \zeta)(1 - J) C[\rho, J, l, t]),
\] (37)

where \(C\) is the following functional of the density:

\[
C[\rho, J, l, t] = \int_{0}^{t} \frac{-l - \beta \rho(s) q(l)}{l(1 - J) - (1 + \zeta - l)} e^{vl - \zeta t} ds.
\] (38)

### 4.2 Closure condition on the density

The definition of the density at time \(t\), equation (18), induces the following consistency condition, based on the derivative of the generating function \(w.r.t.\ J\), expressed in the functional form we have just obtained in equation (36):

\[
\rho(t) = \int_{0}^{l} dl \frac{\partial}{\partial J} |_{l=1} \left[ H \left( 1 - \frac{(1 - J)(l - 1 - \zeta)}{l(1 - J) - (l(1 - J) + (1 + \zeta - l)) e^{vl - 1 - \zeta t}, l, 0} \right) \right]
\]

\[
+ \int_{0}^{l} dl H(l, 0) \frac{\partial}{\partial J} |_{l=1} \left( \exp((l - 1 - \zeta)(1 - J) C[\rho, J, l, t]) \right).
\] (39)
The normalisation condition of the probability distribution \( p_l \) of occupation numbers at level \( l \) reads (at time 0):

\[
H(1, l, 0) = 1. \tag{40}
\]

The derivative needed in the integrand of the first term in equation (39) is obtained from a Taylor expansion at first order in \( h \) for \( J = 1 + h \) (for negative \( h \)):

\[
H \left( 1 - \frac{-h(l - 1 - \zeta)}{-hl - (-hl + (1 + \zeta - l))e^{l+\zeta-1-J}, l, 0} \right) = H(1, l, 0)
\]

\[
+ e^{-(l+\zeta-1)j} \frac{\partial}{\partial j} \left[ H(J, l, 0) + O(h) = 1 + e^{-(l+\zeta-1)h} \pi_l(0) + O(h), \right. \tag{41}
\]

We read off

\[
\frac{\partial}{\partial j} \left|_{\ j=1} \right. \left. \left[ H \left( 1 - \frac{1-J(l-1-\zeta)}{l(l-1-J) - (l(l-1-J) + (1 + \zeta - l))e^{l+\zeta-l-1}, l, 0} \right) \right] = e^{-(l+\zeta-1)j} \pi_l(0). \right. \tag{42}
\]

On the other hand, the factor of \((1 - J)\) in the argument of the exponential of the second term of equation (39) yields immediately

\[
\frac{\partial}{\partial j} \left|_{\ j=1} \right. \left. (\exp(l - 1 - \zeta)(1 - J) C[\rho, J, l, t]) = -(l - 1 - \zeta) C[\rho, 1, l, t]. \right. \tag{43}
\]

We therefore find the following closure condition on the density:

\[
\rho(t) = \int_0^1 e^{-(l+\zeta-1)j} \pi_l(0) dl - \int_0^1 (l - 1 - \zeta) C[\rho, 1, l, t] dl. \tag{44}
\]

This integral condition is a Volterra equation:

\[
\rho(t) = z(t) + (K^* \rho)(t), \tag{45}
\]

where the function \( z \) contains the initial conditions

\[
z(t) = \int_0^1 e^{-(l+\zeta-1)j} \pi_l(0) dl + \int_0^t \left( \int_0^l ds \beta e^{l+\sigma-1-\zeta}(s) \right) dl, \tag{46}
\]

and the kernel \( K \) depends only on the density \( q \) and the rates of the three stochastic processes:

\[
K(T) := \beta \int_0^T q(l) e^{l+\sigma-1-\zeta} dl. \tag{47}
\]

Let us denote the Laplace transform of a function \( f \) of time as follows:

\[
\hat{f}(s) = \int_0^\infty e^{-st} f(t) dt. \tag{48}
\]

The Laplace transform of the convolution equation satisfied by the density yields the following expression for the Laplace transform of the density, in terms of the parameters of the process and the initial conditions:

\[
\tilde{\rho}(s) = \frac{\hat{z}(s)}{1 - \hat{K}(s)} \tag{49}
\]

4.3. Expectation value of the occupation number at a fixed fitness level

We can adapt the derivation of the consistency equation (equation (39)) to obtain the expectation value \( \bar{\pi}_l \) of the number of particles at a fixed fitness level \( \bar{l} \):

\[
\bar{\pi}(t) = \frac{\partial}{\partial j} \left|_{\ j=1} \right. \left. H(J, l, t) \right.
\]

\[
= \frac{\partial}{\partial j} \left|_{\ j=1} \right. \left. \left[ H \left( 1 - \frac{(1-J)(l-1-\zeta)}{l(l-1-J) - (l(l-1-J) + (1 + \zeta - l))e^{l+\zeta-1-J}, l, 0} \right) \right. \right.
\]

\[
+ H(1, l, 0) \frac{\partial}{\partial j} \left|_{\ j=1} \right. \left. ((\exp(l - 1 - \zeta)(1 - J) C[\rho, J, l, t])) \right.
\]

\[
\left. = e^{-(l+\zeta-1)j} \pi_l(0) - (l - 1 - \zeta) C[\rho, 1, l, t] \right.
\]

\[
= e^{-(l+\zeta-1)j} \pi_l(0) + \left( \int_0^t ds (l + \beta \rho(s) q(l)) e^{l+\zeta-1-J}(s) \right). \tag{50}
\]

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We can adapt the derivation of the consistency equation (equation (39)) to obtain the expectation value \( \bar{\pi}_l \) of the number of particles at a fixed fitness level \( \bar{l} \):

\[
\bar{\pi}(t) = \frac{\partial}{\partial j} \left|_{\ j=1} \right. \left. H(J, l, t) \right.
\]

\[
= \frac{\partial}{\partial j} \left|_{\ j=1} \right. \left. \left[ H \left( 1 - \frac{(1-J)(l-1-\zeta)}{l(l-1-J) - (l(l-1-J) + (1 + \zeta - l))e^{l+\zeta-1-J}, l, 0} \right) \right. \right.
\]

\[
+ H(1, l, 0) \frac{\partial}{\partial j} \left|_{\ j=1} \right. \left. ((\exp(l - 1 - \zeta)(1 - J) C[\rho, J, l, t])) \right.
\]

\[
\left. = e^{-(l+\zeta-1)j} \pi_l(0) - (l - 1 - \zeta) C[\rho, 1, l, t] \right.
\]

\[
= e^{-(l+\zeta-1)j} \pi_l(0) + \left( \int_0^t ds (l + \beta \rho(s) q(l)) e^{l+\zeta-1-J}(s) \right). \tag{50}
\]
The expectation value of the occupation number at fitness level $l$ therefore forgets the initial condition $\pi_l(0)$ at an exponential rate, which decreases linearly with the fitness:

$$\tilde{\pi}_l(t) = e^{-(l+\zeta-1)l}\tilde{\pi}_l(0) + \left(1 - le^{-(l+\zeta-1)l}\right) + \beta q(l) \int_0^t e^{(l+\zeta-1)(t-s)}\rho(s)ds.$$  \hfill (51)

The Laplace transform of exponential functions,

$$\int_0^\infty e^{-st}e^{rs}dt = \frac{1}{s-a},$$  \hfill (52)

yields the following expression for the Laplace transform of the average occupation number at fitness level $l$, for $s > 0$:

$$\tilde{\pi}_l(s) = \left(\pi_l(0) - \frac{l}{1 + \zeta - l}\right)s + 1 + \zeta - l + \frac{l}{1 + \zeta - l}s + \beta q(l)s - \beta q(l)s\tilde{\beta}(s).$$  \hfill (53)

As we have expressed the Laplace transform $\tilde{\rho}$ of the density in equation (49), the expectation value $\tilde{\pi}_l$ is completely characterised by equation (53) in the Laplace domain. Inverting the Laplace transform of the density would yield an expression for $\tilde{\pi}_l$ as a function of time. However, the explicit result we have obtained in the Laplace domain has a direct application to a system undergoing resetting at random times distributed with a constant rate.

5. Resetting events

5.1. Review of the renewal argument

Let us consider the system of particles evolving according to the processes we described in section 2, but assume it is reset to its initial configuration at random times. This configuration is given by the number of particles in every state, which induces the collection of occupation numbers at every fitness level.

Assume the resetting events occur at a fixed rate $r$. The configurations of the system under resetting are the same as the ones in the system with no resetting, but they have different probabilities. For a fixed configuration, let us denote by $P_l(t)$ the probability of this configuration in the system undergoing resetting at rate $r$ (and by $P_0(t)$ the probability of this configuration in the system without resetting), conditional on the fixed initial configuration to which the system is instantaneously brought back at each resetting event. Following the renewal argument of [29, 32], the probability distribution $P_l(t)$ can be expressed in terms of the probability distribution $P_0$. The expression consists of two terms corresponding to the following alternative. There has been either no resetting event in the time interval $[0, t]$ (the probability of this event is $e^{-rt}$), or the last resetting event occurred within an infinitesimal time $dt$ of $t - \tau$, for some value of $\tau$ in $[0, t]$ (the probability density of this event is $r e^{-rt}dt$). Conditioning on these events yields:

$$P_l(t) = e^{-rt}P_0(t) + r \int_0^t e^{-r\tau}P_0(\tau)d\tau.$$  \hfill (54)

The large-time limit of this equation shows that the Laplace transform of the ordinary probability distribution yields the steady-state probability distribution of the system under resetting.

5.2. Application to the steady state of the system under resetting

Let us apply this very general argument to our model. Consider a fitness level $l$ and an integer $k \geq 0$, and denote by $P_0(k, t, l)$ the probability of the presence of $k$ particles at fitness level $l$ at time $t$ (conditional on a fixed configuration at time zero), in the absence of resetting. Let us denote by $P_l(k, t, l)$ the probability of the same event (conditional on the same initial condition), in the presence of resetting at rate $r$. With this notation the probability distribution satisfying the master equation (equation (13)) reads $p_l(k, t) = P_0(k, t, l)$.

Rewriting the renewal equation (54) in our notations, we obtain:

$$P_l(k, t, l) = e^{-rt}P_0(k, t, l) + r \int_0^t e^{-r\tau}P_0(k, \tau, l)d\tau, \quad \forall k \geq 0, \quad \forall l \in (0, 1).$$  \hfill (55)

The expectation value of the occupation number of fitness level $l$ under resetting is therefore expressed as:

$$\sum_{k \geq 0} kP_l(k, t, l) = e^{-rt} \sum_{k \geq 0} kP_0(k, t, l) + r \int_0^t e^{-r\tau} \sum_{k \geq 0} P_0(k, \tau, l)d\tau.$$  \hfill (56)

Let us introduce the following notation:

$$\pi_{lt}(t) = \sum_{k \geq 0} kP_l(k, t, l).$$  \hfill (57)

Let us keep the notation $\pi_l$ introduced in equation (18) for the expectation value of the occupation number at level $l$ in the absence of resetting (even though the notation $\pi_{lt}$ would also be consistent for this quantity), and rewrite the renewal equation (equation (58)):
\[ \rho_\ell(t) = e^{-rt} \rho_\ell(t) + r \int_0^t e^{-r(\tau-t)} \bar{\rho}_\ell(\tau) d\tau. \]  

Consider the steady state of the system under resetting. The expectation value of the number of particles at fitness level \( l \) is read off from the large-time limit of equation (58) in terms of the Laplace transform of \( \bar{\rho}_\ell \):

\[ \bar{\rho}_\ell(\infty) = r \bar{\rho}_\ell(r). \]  

The expression needed on the r.h.s. was worked out in equation (53) when we took the Laplace transform of the convolution equation satisfied by \( \bar{\rho}_\ell \). We therefore read off

\[ \bar{\rho}_\ell(\infty) = \left( \bar{\rho}_\ell(0) - \frac{r}{1 + \zeta - l} \right) \bar{\rho}_\ell(r) + \frac{r}{1 + \zeta - l} \beta q(l) \bar{\rho}(r). \]  

Integrating (61) w.r.t. fitness yields the expression of the steady-state density \( \rho_\ell(\infty) \) in terms of the Laplace transform of the ordinary density:

\[ \rho_\ell(\infty) = \int_0^1 \bar{\rho}_\ell(\infty) dl = r \int_0^1 \bar{\rho}(r) dl = r \bar{\rho}(r). \]  

The average occupation number at level \( l \) in the steady state of the system under resetting contains a skewed version of the density \( q \), weighted by the hopping rate \( \beta \) and the average steady-state density of the system. Moreover, the resetting rate combines with the sum of hopping and death rates, to yield a factor with the same structure as in the steady state without resetting (Equation (14)):

\[ \bar{\rho}_\ell(\infty) = \frac{l + r \bar{\rho}_\ell(0)}{1 + \zeta + r - l} + \frac{\beta q(l)}{1 + \zeta + r - l}. \]  

The density parameter \( \rho_\ell(\infty) \) can be expressed using the consistency condition,

\[ \rho_\ell(\infty) = \int_0^1 \bar{\rho}_\ell(\infty) dl, \]  

which yields

\[ \rho_\ell(\infty) = \left( \int_0^1 \frac{l + r \bar{\rho}_\ell(0)}{1 + \zeta + r - l} dl \left( 1 - \beta \int_0^1 \frac{q(l) dl}{1 + \zeta + r - l} \right) \right)^{-1}. \]  

If \( \beta \) is below the critical value worked out in the absence of resetting (equation (16)), the denominator in the above quantity is positive. On the other hand, the density \( \rho_\ell(\infty) \) can be predicted by the Laplace transform of the Volterra equation, using equations (46), (47), (49):

\[ \bar{\rho}(r) = \int_0^1 \frac{\bar{\rho}_\ell(0) dl}{1 + \zeta + r - l} + \int_0^1 \frac{1}{r} \int_0^1 \frac{l dl}{1 + \zeta + r - l} \]  

\[ = \int_0^1 \frac{\bar{\rho}_\ell(0) dl}{1 + \zeta + r - l} + \int_0^1 \frac{1}{r} \int_0^1 \frac{q(l) dl}{1 + \zeta + r - l}, \]  

\[ \bar{\rho}(r) = \beta \int_0^1 \frac{q(l) dl}{1 + \zeta + r - l}, \]  

\[ r \bar{\rho}(r) = \frac{1}{1 - \beta \int_0^1 \frac{q(l) dl}{1 + \zeta + r - l}} \int_0^1 \frac{(r \bar{\rho}_\ell(0) + l) dl}{1 + \zeta + r - l}, \]  

which confirms the value obtained from the consistency condition (using equation (61) relating the steady-state density to the Laplace transform of \( \rho \) at the resetting rate).

6. Conclusions

We have expressed the generating function of a non-conserving ZRP with extensive rates as a functional of the average density. The density satisfies an integral equation of Volterra type. This equation implies that the expectation value of the occupation number of a given fitness level goes to its steady-state value at an exponential rate that decreases linearly with the fitness. Moreover, the Volterra equation satisfied by the density is enough to characterise the expectation value of the occupation number at every fitness level in the Laplace domain.

We obtained the expectation values of the occupation numbers at each fitness level of the system under stochastic resetting at constant rate. They are induced by the values of the Laplace transform of the ordinary occupation numbers, evaluated at the resetting rate \( r \). The result has a very simple structure that interpolates
between the initial conditions (at strong resetting) and the ordinary case (at zero resetting). The hopping process can be mapped to a set of independent random walkers on a fully connected, large set of states. Recent developments on stochastic resetting of interacting particle systems have addressed properties of the symmetric exclusion process [36] and totally asymmetric exclusion process [42], and in [43], the phase diagram in the plane of temperature and resetting rate has been presented for the Ising model, an interacting system with a thermodynamic phase transition in its equilibrium state. However, the present model allows for a mapping of the model of growing networks, as well as to a microscopic version of Kingman’s house-of-cards model.

Indeed the system can be interpreted as a model of the balance of selection and mutation, or (by mapping particles to oriented links), as a model of a network in which the links can form at a rate given by the fitness level, vanish at a fixed rate $\delta$, and be randomly rewired at a rate $\beta$. The model then becomes a version of the Bianconi–Barabási model with random rewiring of the destination of links. The ordinary case, worked out in [2], corresponds to a skewed version of the density of states $q$, with an extra term that gives rise to an atom at maximum density when the sum of the death and hopping rates approaches the maximum production rate (the production rate of particles at maximum fitness, which we set to 1). The resetting process modifies the ordinary formula in two intuitive ways, that are enough to completely recover the result:

1. the resetting rate $r$ adds up to the sum of the death and mutation rates (the combination denoted by $1 + \zeta$ in equation (21)), as one of the processes balancing selection, so that an atom develops at maximum fitness in the limit of zero resetting rate and zero $\zeta$ (in this limit the steady-state density of the system diverges as $-\log(\zeta + r)$);

2. the initial conditions add up to the term $\beta q(r)q(l)$ through the combination $r\Pi(0)$.

The steady-state density $\mu(\infty)$ can be recovered as a consistency condition after applying these two prescriptions to the ordinary expression (even though we obtained it from the Laplace transform of the Volterra equation in the first place). The resetting process at constant rate therefore modifies the house-of-cards effect in the following sense: it combines with the mutation to reshuffle the genomic deck, mixing the mutant density with the initial conditions.

Technically, the Laplace transform of the average occupation numbers was enough to characterise the steady state of the model under resetting, because of the Poisson distribution of the resetting times on which we condition to work out the renewal equation. Inverting the Laplace transform would allow to study the large-time behaviour of the integral of the occupation numbers on a shrinking interval of high fitnesses of the form $[1 - x/t, 1]$. This behaviour would depend on the effective annihilation rate $\beta + \delta$. It would be interesting to let this parameter go to 1 (which leads to the emergence of an atom at maximum fitness due to the first integral in equation (14), and to see whether the large-time limit of the total population in the considered shrinking interval could be expressed as a function of $x$ only. This is the case in the Kingman house-of-cards model, in which this function is related to the incomplete gamma function, provided the mutant density vanishes as a power law at maximum fitness [44]. This gamma-wave shape has been shown to occur in other processes exhibiting condensation [14, 45].

The resetting events we considered leave the set of states fixed. In population dynamics, this corresponds to a fixed mutant density. We assumed this density to vanish at maximum fitness, which is equivalent to a vanishing probability of a beneficial mutation at high values of fitness. The condensate in the house-of-cards model [19] is indeed an effect of selection only. However, the emergence of beneficial mutations can be modelled by new values of fitness drawn from a mutant density with an unbounded support. Such a model was studied in [46] for a measure-valued model in the limit of an infinite population. Adapting the present model to such a mutant density would require to give a prescription for the gradual introduction of states in the system, because starting with states of arbitrarily high reproductive fitness would quickly give rise to divergences in the occupation numbers. Moreover, a more radical resetting prescription would involve a complete destruction of particles and states. The hopping process would take place on a growing lattice that would approach the underlying mutant density, until the next resetting event interrupts this growth process.

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