Steady states in a non-conserving zero-range process with extensive rates as a model for the balance of selection and mutation

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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 removed from the system with a uniform annihilation rate. On a fully-connected lattice with a large number of sites, the probability of configurations is assumed to factorise in the steady state. This mean-field approximation 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 of particles is mapped to a model of population dynamics: the site label is interpreted as a level of fitness, the site-dependent creation rate is interpreted as a selection function, and the hopping process is interpreted as the introduction of mutants. In the limit of a large density, the average fraction of the total population occupying each site approaches the limiting distribution in the house-of-cards model of selection-mutation, introduced by Kingman. A single site can be occupied by a macroscopic fraction of the particles if the mutation rate is below a critical value (which matches the critical value worked out in the house-of-cards model). This feature generalises to classes of selection functions that increase sufficiently fast at high values of fitness.

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1 Introduction and background

Condensation is a feature of steady states of a variety of out-of-equilibrium systems, including granular materials, traffic flows and distributions of wealth. Some models of non-equilibrium statistical mechanics with particles distributed over a large number of sites can exhibit condensation as the macroscopic occupation of a single site \[1-3\]. A prominent class of such models is based on the zero-range process (ZRP) \[4-7\], in which particles hop from any site at a rate \(u\) depending only on the number of particles \(n\) at this site. If \(u\) is an increasing function, no condensate can form, but for rates of the form

\[
u_b(n) = \left(1 + \frac{b}{n}\right) \theta(n), \tag{1}\]

where \(\theta\) is the Heaviside step function, lead to the formation of a condensate if \(b > 2\). Once it is formed, the condensate can undergo an ergodic motion, or be trapped at a site in the case of inhomogeneous hopping rates \[8-11\].

In \[12, 13\], a non-conserving version of the ZRP was introduced, with particles added to each site at a constant rate, and particles removed from each site at a rate increasing (as a power law) with the number of particles present at the site. The functional form of these rates was chosen to be the same for all sites. The hopping rate was of the decreasing form given in Eq. 1. The model was studied on a large lattice using a mean-field approximation. The phase diagram, which includes a super-extensive high-density phase, was worked out in terms of the scaling behaviour of the hopping current at large system size.

On the other hand, Kingman \[14\] introduced a deterministic measure-valued model of the competition between selection and mutation in the fitness distribution in a large haploid population, which exhibits a condensation phenomenon if the mutation rate is small enough. The fitness of individuals is modelled as a single bounded number: at generation \(n\), the fitness distribution is a probability measure \(p_n\) on the interval \([0, 1]\). The model assumes that the next generation consists of a fraction \(\beta\) of mutants, whose fitness distribution is a fixed probability measure \(q\) on \([0, 1]\), and of descendants of the previous generation, contributing a skewed term proportional to \((1 - \beta)xp_n(dx)\). The factor of \(x\) reflects the higher reproduction rate of individuals with higher fitness. Normalisation of the measure \(p_{n+1}\) induces the recurrence relation

\[
p_{n+1}(dx) = (1 - \beta) \frac{xp_n(dx)}{\int_{[0,1]} xp_n(dx)} + \beta q(dx). \tag{2}\]

If the mutation rate \(\beta\) is lower than a critical value (depending only on the mutant fitness \(q\), the
limiting distribution develops an atom at the maximum value of fitness:

\[ p_\infty(dx) = \frac{\beta q(dx)}{1 - x} + \left(1 - \frac{\beta}{\beta_c}\right) \delta_1, \quad \text{if} \quad \beta < \left(\int_{[0,1]} \frac{q(dx)}{1 - x}\right)^{-1}. \quad (3) \]

This model is termed the house-of-cards model as mutations reshuffle the genomic deck: the steady distribution of fitness is a skewed version of the mutant fitness \( q \). The emergence of the condensate exhibits universality properties depending only on the local behaviour of the mutant fitness \( q \) at high fitness \([15, 16]\). Making the house-of-cards model more realistic involves the introduction of randomness (see \([17]\) for rigorous developments on random mutation rates, and \([18]\) for applications to the Lenski experiment studying the fitness of a growing bacterial population through regular sampling). The introduction of new mutants, as well as the births and deaths of individuals, can be modelled as Markovian processes, and the steady state of the system could be characterised by the probability law of the number of individuals at each fitness level. This would allow for instance to estimate the fluctuations of the population at each level of fitness. 

In this paper we consider a non-conserving zero-range process with a large number of sites, and map it to a model of selection and mutation. Hopping rates model mutation, inhomogeneous creation rates model selection, and homogeneous annihilation rates model death. The hopping rates are not assumed to be of the form given in Eq. \([1]\) but are chosen to be proportional to the number of particles:

\[ u(n) := \beta n, \quad (4) \]

where the factor \( \beta \) models the mutation rate. Such hopping rates could not lead to a condensate in the case of the conserving ZRP \([3]\). In the limit of a large number \( L \) of sites, the site labels (divided by \( L \)) can be thought of as fitness levels that can approach any value in the interval \([0,1]\). The introduction of randomness in the evolution of the system avoids the partition of the population into generations. Moreover, it should allow to work out the probability law of the number of individuals at each fitness level in a steady state. If mutants are allowed to hop from a site to any other site, each site has many neighbours in the large-\( L \) limit, and approximations inspired by mean-field theory are expected to give good results, as in \([12,13]\).

In Section 2 we will describe the model more completely and set up notations. In Section 3 we will write the steady-state master equation, assuming the numbers of particles at all sites to be independent. In Section 4 we will solve this equation and the steady-state numbers of particles will appear to be to be negative binomial variables, with site-dependent parameters. In Section 5 we will work out the average fraction of all particles occupying each site in a simple case, and identify a regime of parameters in which the average density goes to infinity, while a finite fraction of the particles is concentrated at the highest fitness value. The ratio of the average number of individuals at a given fitness level to the average density will be related to the skewed large-time distribution appearing in the deterministic house-of-cards model (Eq. \([3]\)). In Section 6 we will choose parameters and present numerical simulations at large but finite \( L \). In Section 7 the model will be generalised, based on features depending only on the local behaviour of the creation rate and mutant fitness.
2 Non-conserving ZRP with extensive, inhomogeneous rates

Consider a lattice of $L$ sites, with site labelled $l$ carrying a random number $n_l$ of particles. We use the site label to model the fitness level of individuals in a haploid population: there are $n_l$ individuals with fitness level $l/L$ (so that in the large-$L$ limit the fitness can be arbitrarily close to any value in the interval $[0, 1]$). The number $n_l$ can evolve due to annihilation, creation and hopping from site to site. These three processes model deaths, births and mutations in the population. The rates of the processes (i.e. their probabilities per unit of time) are chosen as follows.

Particles are annihilated at each site at a rate proportional to the number of particles at the site, with a proportionality factor $\delta > 0$, independent of the site label:

$$n_l \to n_l - 1 \text{ with rate } \delta n_l, \text{ for all } n_l > 0. \quad (5)$$

Particles are created at site labelled $l$, at a rate chosen to be an increasing positive function $f$ of the fitness level $l/L$:

$$n_l \to n_l + 1 \text{ with rate } f(l/L)(n_l + 1), \text{ for all } n_l \geq 0. \quad (6)$$

where the shift in the factor $(n_l + 1)$ is introduced in order to prevent the state with no particles at any site from being steady. One can think of this shift as modelling the action of an external agent, who introduces one particle at any empty site, at a site-dependent rate adjusted to maintain the creation rates of the selection process. The function $f$ will be referred to as the selection function, as it models the higher reproduction rate of individuals with higher fitness. We will assume that $f(1) = 1$ (this assumption is equivalent to setting the time scale so that one particle is created on average per unit of time at the site of maximum fitness, labelled $l = L$, if this level of fitness contains no particle).

The hopping process is a zero-range process: particles hop from site labelled $l$ at a rate depending only on the number of particles present at the site. Let us choose an extensive hopping rate:

$$u(n) = \beta n, \quad \beta > 0. \quad (7)$$

The positivity constraint on the number of particles that has to be imposed through a factor of $\theta(n)$ in the decreasing hopping rate of Eq. 1, is automatically satisfied.

When a particle hops from site $l$, the destination site is chosen randomly among the other $L - 1$ sites, with a probability law derived from a fixed probability measure $(q_m)_{1 \leq m \leq L}$, i.e. $q_m \geq 0$ and $\sum_{m=1}^{L} q_m = 1$. In the large-$L$ limit we will pick these numbers as special values of a smooth probability density $q$ on the interval $[0, 1]$:

$$q_l := \frac{q(l/L)}{\sum_{j=1}^{L} q(j/L)} \sim_{L \to \infty} \frac{1}{L} q(l/L). \quad (8)$$

The corresponding hopping processes from site $l$ to site $m \neq l$ are therefore described by:

$$(n_l, n_m) \to (n_l - 1, n_m + 1) \text{ with rate } \beta n_l \frac{q_m}{1 - q_l}, \quad (9)$$
where the denominator in the rate ensures normalisation of the probability law of the destination site. These processes model the production of mutants in the population, and the density $q$ is the probability density of the fitness of the new mutants. It will be referred to as the mutant density. Moreover, we will assume that $q(1) = 0$ (new mutants have zero probability of having maximum fitness).

The list of parameters of the model therefore consists of a large integer $L$, two positive numbers $\beta$ (the mutation rate) and $\delta$ (the death rate, or annihilation rate), a smooth probability density $q$ (the mutant density) on the interval $[0,1]$, satisfying $q(1) = 0$, and a positive increasing function $f$ (the selection function) on the interval $[0,1]$, satisfying $f(1) = 1$.

### 3 Mean-field approximation and steady-state equations

Let us postulate that the steady-state probability of each configuration of the system factorises: we assume the existence of $L$ probability distribution functions, denoted by $(p_l)_{1 \leq l \leq L}$, such that

$$P(n_1, \ldots, n_L) = \prod_{l=1}^{L} p_l(n_l). \quad (10)$$

The conserving zero-range process is known to exhibit such a factorised steady-state probability distribution [6]. In the non-conserving case, the factorisation is a mean-field assumption, which is expected to be good if each site has a large number of neighbours connected to it by the hopping process (Eq. 9), which is the case if the probability density $q$ is supported on the entire interval $[0,1]$. This approximation was made in [13] in the case of translation-invariant creation, annihilation and hopping rates.

For a fixed site labelled $l$, let us write schematically the steady-state master equation as

$$\frac{dp_l}{dt}(n) = 0 = A_l(n) + C_l(n) + M_l(n), \quad \forall n \geq 0, \quad (11)$$

where the annihilation, creation and mutation terms are denoted by $A_l$, $C_l$ and $M_l$ respectively.

Based on the translation-invariant death rates of Eq. 5, the annihilation term reads

$$A_l(n) = \delta \{ (n+1)p_l(n+1) - n\theta(n)p_l(n) \}, \quad (12)$$

where the factor $\theta(n)$ imposes that there should be at least one particle on site before annihilation takes place (even though this constraint is redundant because of the factor of $n$ from the annihilation rate).

Based on the fitness-dependent creation rates of Eq. 6, the creation term reads

$$C_l(n) = f(l/L) \{ \theta(n)np_l(n-1) - (n+1)p_l(n) \}, \quad (13)$$
where the factor $\theta(n)$ imposes that there should be at least one particle on site after creation has taken place.

In the large-$L$ limit, the flow of particles to site $l$ per unit of time is proportional to $q(l/L)$ and to the average density $\rho$ of the system:

$$\rho := \frac{1}{L} \sum_{k=1}^{L} \bar{n}_k, \quad \bar{n}_k := \sum_{n \geq 0} np_k(n).$$

Indeed the contribution of the normalisation factors in the hopping rates to site labelled $l$ (Eqs 8 and 9) are negligible in the large-$L$ limit:

$$\beta q_l \left( \sum_{k \neq l} \sum_{n_k \geq 0} \frac{1}{1 - q_k} n_k p_k(n_k) \right) \simeq_{L \to \infty} \beta \frac{1}{L} q(l/L) \sum_{k \neq l} \left( \bar{n}_k + \frac{1}{L} \bar{m}_k q(k/L) + o(L^{-1}) \right)$$

$$= \beta \rho q(l/L) + o(1).$$

The mutation term in the steady-state master equation therefore reads:

$$M_l(n) = \beta \left\{ (n + 1)p_l(n + 1) - n\theta(n)p_l(n) \right\} + \rho q(l/L) (\theta(n)p_l(n - 1) - p_l(n)),$$

where the factors of $\theta(n)$ impose there should be least one particle on site when a particle hops from the site (even though this constraint is redundant in one case because of the factor of $n_l$ in the hopping rate).

There are therefore four terms with constraints and four terms without constraint in each of the steady-state conditions:

$$0 = \theta(n) \left\{ (\beta \rho q(l/L) + f(l/L)n) p_l(n + 1) - (\delta + \beta)np_l(n) \right\}$$

$$+ (\beta + \delta)(n + 1)p_l(n + 1) - (\beta \rho q(l/L) + f(l/L)(n + 1)) p_l(n), \quad \forall n \geq 0. \quad (17)$$

For $n = 0$ the steady-state condition reduces to

$$p_l(1) = \frac{\beta \rho q(l/L) + f(l/L)}{\beta + \delta} p_l(0), \quad (18)$$

so that at any value of $n$ the constrained and unconstrained parts of the balance equation (Eq. 17) are separately equal to zero. This reproduces the structure of the mean-field master equation derived in [13] in the case of homogeneous rates, where only one probability law needs to be determined to express the probability of any configuration. By induction on $n$ we therefore obtain:

$$p_l(n) = \prod_{k=1}^{n} \frac{\beta \rho q(l/L) + f(l/L)k}{(\beta + \delta)k} p_l(0). \quad (19)$$

The normalisation factors $(p_l(0))_{1 \leq l \leq L}$ and the average density $\rho$ still have to be fixed.
4 Normalisation and average density

Let us factorise the selection function in the expression of $p_l(n)$ and introduce the Pochhammer symbol

$$(a)_n := a \times (a + 1) \times \cdots \times (a + n - 1) = \frac{\Gamma(a + n)}{\Gamma(a)}.$$  

(20)

$$p_l(n) = p_l(0) \prod_{k=1}^{n} \frac{\beta q(l/L) + f(l/L)k}{(\delta + \beta)k} = p_l(0) \left( \frac{f(l/L)}{\delta + \beta} \right)^n \frac{1}{n!} \left( \frac{\beta q(l/L)}{f(l/L)} + 1 \right)^n.$$  

(21)

Using the identity

$$\frac{1}{(1-z)^a} = 1 + \sum_{n \geq 1} \frac{(a)_n}{n!} z^n, \quad |z| < 1,$$  

(22)

we can express the normalisation factor at site labelled $l$, provided $\delta + \beta > 1$ (which condition ensures convergence of the sum at all sites because $f(1) = 1$ is the maximum of the selection function). Defining a parameter $\zeta > 0$ by

$$\delta + \beta = 1 + \zeta,$$  

(23)

we obtain the normalisation factor (in terms of the still-unknown density $\rho$) as:

$$p_l(0) = \left( 1 - \frac{f(l/L)}{1 + \zeta} \right)^{\frac{\beta q(l/L)}{f(l/L)} + 1}.$$  

(24)

Moreover, we can recognise $p_l$ as a negative binomial law

$$p_l(n) = \frac{1}{n!} (r_l)_n \pi_l^n (1 - \pi_l)^n,$$  

(25)

with parameters depending on the fitness level:

$$\pi_l = 1 - \frac{f(l/L)}{1 + \zeta}, \quad r_l = 1 + \beta \rho \frac{q(l/L)}{f(l/L)}.$$  

(26)

We deduce an expression of the mean value of the number of particles at site labelled $l$, in which the only unknown parameter is the average density:

$$\bar{n}_l = \sum_{n > 0} np_l(n) = r_l \frac{1 - \pi_l}{\pi_l},$$  

(27)

$$\bar{n}_l = \beta \rho \frac{q(l/L)}{1 + \zeta - f(l/L)} + \frac{f(l/L)}{1 + \zeta - f(l/L)}.$$  

(28)

We can already see that for $l < L$, the first term (which is a skewed version of the mutant density) will be dominant if the density $\rho$ is large. Moreover, the assumption $q(1) = 0$ implies that the number of particles at the maximum fitness level follows a geometric law, and $\bar{n}_L = \zeta^{-1}$. Values of $\zeta$ larger than 1 can therefore be considered large for our purposes, and we observe that values of
ζ close to zero yield large numbers of particles at maximum fitness. Indeed the site labelled \( l = L \) does not receive any particle from the mutation process, and at this site \( \beta + \delta = 1 + \zeta \) combine as an effective total annihilation rate, while the local creation rate is \( f(1) = 1 \).

Consistency with the definition of the average density \( \rho \) (Eq. 14) yields, rewriting Riemann sums as integrals using the large-\( L \) limit:

\[
\rho = \frac{1}{L} \sum_{l=1}^{L} \frac{f(l/L)}{1 + \zeta} \left( \beta \frac{q(l/L)}{f(l/L)} + 1 \right) \left( 1 - \frac{f(l/L)}{1 + \zeta} \right)^{-1}
\]

\[
\simeq_{L \to \infty} \beta \rho \int_{0}^{1} \frac{q(x)dx}{1 + \zeta - f(x)} + \int_{0}^{1} \frac{f(x)dx}{1 + \zeta - f(x)}.
\]

As \( \zeta > 0 \) and \( f(1) = 1 \) is the maximum of the selection function, all the integrands in the above expression are positive. The average density \( \rho \) can therefore only be positive if

\[
\beta \int_{0}^{1} \frac{q(x)dx}{1 + \zeta - f(x)} < 1.
\]

Considering the parameter \( \zeta \) as fixed, we can rewrite this condition (using Eq. 23) as a lower bound on the death rate:

\[
\delta > \delta_c(\zeta), \quad \text{with} \quad \delta_c(\zeta) = 1 + \zeta - \left( \int_{0}^{1} \frac{q(x)dx}{1 + \zeta - f(x)} \right)^{-1}.
\]

The average density can therefore be expressed in terms of the mutant density, selection function, and two parameters \( \zeta \) and \( \epsilon \) that depend only on the pair \( (\beta, \delta) \)

\[
\rho = \frac{1}{\epsilon} \left( \int_{0}^{1} \frac{q(x)dx}{1 + \zeta - f(x)} \right)^{-1} \int_{0}^{1} \frac{f(x)dx}{1 + \zeta - f(x)}, \quad \zeta = \delta + \beta - 1 > 0, \quad \epsilon = \delta - \delta_c(\zeta) > 0.
\]

5 Example: linear selection function

In the house-of-cards model of selection and mutation [14], the individuals that do not undergo mutation have a number of descendants that is proportional to their fitness. This motivates us to choose

\[
f(x) := x.
\]

We would like to define the mutant density \( q \) so that the integral in the definition of \( \delta_c(\zeta) \) in Eq. 31 has a finite limit when \( \zeta \) goes to zero. Otherwise \( \delta_c(0) \) would equal 1 and the corresponding mutation rate would be zero. For this purpose it is enough to choose \( q \) with the following local behaviour at high values of fitness:

\[
q(1 - h) = O(h^{\alpha}), \quad \text{where} \quad \alpha > 0.
\]
With such a choice of mutant density, \( \beta \) goes to a strictly positive limit if the parameter \( \zeta \) goes to zero at fixed \( \epsilon > 0 \), hence the notation:

\[
\beta_c := \left( \int_0^1 \frac{q(x)dx}{1 - f(x)} \right)^{-1}, \quad \lim_{\zeta \to 0, \text{fixed } \epsilon} \beta = \beta_c - \epsilon.
\] (35)

We recognise \( \beta_c \) as the critical value of the mutation rate that appears in the house-of-cards model (see Eq. 3).

The average density \( \rho \) can be expressed for this particular choice of \( f \) using Eq. 32. It diverges logarithmically when the parameter \( \zeta \) goes to zero:

\[
\rho(\epsilon, \zeta) = \frac{1}{\epsilon} \left( \int_0^1 \frac{q(x)dx}{1 + \zeta - x} \right)^{-1} \left( -(1 + \zeta) \log \left( \frac{\zeta}{1 + \zeta} \right) - 1 \right),
\] (36)

\[
\rho(\epsilon, \zeta) \sim_{\zeta \to 0^+} -\frac{1}{\epsilon} \beta_c \log \zeta.
\] (37)

Consider the average number of particles at site labelled \( l = xL \), for \( x \) in \([0, 1]\), denoted in the large-\( L \) limit by \( \bar{n}(x) \), divided by the average density. Its expression consists of two terms. One is absolutely continuous with respect to the mutant density \( q \), even at \( \zeta = 0 \), and the other converges to a Dirac measure at maximal fitness value when \( \zeta \) goes to zero:

\[
\frac{\bar{n}(x)}{\rho(\epsilon, \zeta)} = \left( \int_0^1 \frac{q(x)dx}{1 + \zeta - x} \right)^{-1} \left( \frac{q(x)}{1 + \zeta - x} + \frac{1}{\rho(\epsilon, \zeta)} \frac{x}{1 + \zeta - x} \right).
\] (38)

Indeed, if \( \phi \) is a smooth test function on the interval \([0, 1]\), integrating by parts yields:

\[
-\frac{1}{\log \zeta} \int_0^1 \frac{x\phi(x)dx}{1 + \zeta - x} = -\frac{1 + \zeta}{\log \zeta} \left( -\int_0^{1+\zeta} \phi((1 + \zeta)x) dx + \int_0^{1+\zeta} \phi((1 + \zeta)y) dy \right)
\]

\[
= -\frac{1}{\log \zeta} \left( -\log \left( 1 - \frac{1}{1 + \zeta} \right) \phi(1) \right) + o(1)
\]

\[
= \phi(1) + o(1), \quad (\zeta \to 0).
\] (39)

Taking the limit of the expression 38 when \( \zeta \) goes to zero (at fixed \( \epsilon \), using Eqs 35, 37) yields

\[
\lim_{\zeta \to 0, \text{fixed } \epsilon} \frac{\bar{n}(x)}{\rho(\epsilon, \zeta)} = (\beta_c - \epsilon) \frac{q(x)}{1 - x} + \frac{\epsilon}{\beta_c} \delta_1(x),
\] (40)

where we recognise the steady-state measure \( p_\infty \) in the house-of-cards model (Eq. 3), because the quantity \( \beta_c - \epsilon \) is the limit of \( \beta \) when \( \zeta \) goes to zero at fixed \( \epsilon \) (see Eq. 35).

The variance of the negative binomial distribution yields the following expression for the variance of the number of particles at site labelled \( l \)

\[
\text{Var}(n_l) = \frac{\overline{m_l}}{\pi_l} = \frac{(1 + \zeta)\overline{m_l}}{1 + \zeta - f(l/L)}.
\] (41)
At low values of $\zeta$ and $\epsilon$ the average density is large, and the relative fluctuations are proportional to the inverse square root of the density, which realises the thermodynamic limit at fitness level $x < 1$:

$$\frac{\Delta n(x)}{n(x)} \sim \sqrt{\frac{1 + \zeta}{(1 + \zeta - x)n(x)}} \sim_\zeta 0 \sqrt{\frac{-\epsilon}{\beta_c(\beta_c - \epsilon)q(x) \log \zeta}} \sim_\zeta 0, \epsilon < \beta_c \frac{1}{\beta_c} \sqrt{\frac{-\epsilon}{q(x) \log \zeta}}. \quad (42)$$

Because of the local behaviour of the mutant density close the maximum fitness value (Eq. 34), these fluctuations diverge at fixed death and mutation rates when $x$ goes to 1. The fluctuations are therefore concentrated around highest fitness value.

6 Numerical simulations

The non-conserving hopping process can be simulated by picking a (large but finite) value of $L$, a mutant fitness $q$ and a selection function $f$, and by iterating the following steps on an array $(n_l)_{1 \leq l \leq L}$ of integers:

1. calculate the rates of creation, annihilation and hopping at each site (according to Eqs 5,6,7), and concatenate these rates into an array with $3L$ elements;
2. normalise this array and draw an integer in $\{1, \ldots, 3L\}$ with the corresponding probability distribution;
3. read off the event associated with this integer; if this event is a hopping from site $l$, draw the destination site $m \neq l$ from the $L - 1$ remaining sites with probability $q_m(1 - q_l)^{-1}$;
4. update the array $(n_l)_{1 \leq l \leq L}$ accordingly;

The following quadratic choice for the distribution of mutant fitness

$$q(x) := 3(1 - x)^2, \quad (43)$$

leads to an approximately linearly-decreasing first term in the prediction of Eq. 40 if $f(x) = x$, which should be optically detectable for most of the interval $[0, 1]$ if $\zeta$ is small enough. For simulation purposes, the large but finite number $L$ of sites gives a natural scale for the parameter $\zeta$, and we may consider values of $\zeta$ smaller than $1/L$ to be small (see Figs. 1, 2).

The relative fluctuations in Eq. 42 depend on the fitness level $x$, and the upper bound becomes worse when $x$ approaches 1, at fixed values of the death and hopping rates. This upper bound can be used to adjust the parameter $\epsilon$ so that the relative fluctuations do not exceed a certain low threshold $\phi$ in a certain large fraction $\Phi$ of the sites. We therefore picked the following value of $\epsilon$ for numerical simulations:

$$\epsilon := -\beta_c^2 \phi^2 (\min_{x < \phi} q(x)) \log \zeta, \quad (44)$$

with $\phi = 5\%$, and $\Phi = 90\%$ for results reported in Figs. 1, 2).

The empirical results in Fig. 1 reproduce the expected linear profile followed by a sharp knee at high values of the fitness. In Fig. 2 relative fluctuations are observed to form a cloud of points that spreads vertically at large fitness values.
Figure 1: Numerical simulations for $L = 5000$ sites, averaged over 1215 samples, spaced by $10^6$ iterations (red dots). The choice $\zeta = (10L)^{-1}$ yields a predicted average of 50,000 particles at maximum fitness. The choice of quadratic mutant fitness $q$ yields a linearly decreasing profile of $\bar{n}(x)$ for most of the interval $[0, 1]$. 

$L = 5000, \quad \epsilon = 0.0014432, \quad \zeta = 2e^{-05}$

$\beta = 0.66538, \quad f(x) = x$
Figure 2: Fluctuations of densities on $L = 5000$ sites, relative to the averages presented on Fig. 1. The parameter $\epsilon$ was chosen based on the estimate of Eq. 44, controlling the relative fluctuations on $\Phi = 90\%$ of the interval, with $\phi = 10\%$. 

$L = 5000, \ \epsilon = 0.0014432, \ \zeta = 2 \times 10^{-5}$

$\phi = 0.1, \ \Phi = 0.9$
# 7 Generalisation

Going back to the expression of the average density $\rho$ of the system (Eq. 32) for a more general choice of selection function $f$, we observe that an atom developed at the highest fitness value in the above example because the integral

$$ J(f, \zeta) = \int_0^1 \frac{f(x)dx}{1 + \zeta - f(x)} \quad (45) $$

goes to infinity when $\zeta$ goes to zero, which is entirely due to the local behaviour of $f$ at high fitness values.

We can therefore generalise the above results to a one-parameter family of selection functions:

$$ f_\chi(x) = 1 - (1 - x)^\chi, \quad \text{for } \chi > 0, \quad (46) $$

or any selection function with the same local behaviour around 1. The mutant density must satisfy $q(1 - h) = O(h^\alpha)$ with $\alpha > \chi - 1$, so that the critical value of the mutation rate $\beta_c$ is finite.

The dominated convergence theorem implies that the difference

$$ J(f_\chi, \zeta) - \int_0^1 \frac{dh}{\zeta - h^\chi} = -\int_0^1 \frac{h^\chi dh}{\zeta - h^\chi} \quad (47) $$

has a finite limit when $\zeta$ goes to zero. The case $\chi = 1$ studied in the previous example gives rise to a logarithmic divergence, and for $\chi < 1$ the dominated convergence theorem implies that the average density (Eq. 32) has a finite limit when $\zeta$ goes to 0 at fixed $\epsilon$.

For $\chi > 1$, the behaviour of $J(f_\chi, \zeta)$ at small $\zeta$ is therefore the same as that of the subtracted integral in the l.h.s. of Eq. 47 which diverges as $\zeta^{1-\chi}$. To obtain the prefactor, we can first express the relevant integral using hypergeometric series, for large values of $\zeta$:

$$ \int_0^1 \frac{dh}{\zeta - h^\chi} \approx \frac{1}{\zeta} \sum_{k \geq 0} \frac{1}{\chi^k + 1} \left( \frac{-1}{\zeta} \right)^k $$

$$ = \frac{1}{\zeta} \sum_{k \geq 0} \frac{(1)_k}{(1 + \frac{1}{\chi})_k} \frac{1}{k!} \left( \frac{-1}{\zeta} \right)^k $$

$$ = \frac{1}{\zeta} \sum_{k \geq 0} \frac{2F_1 \left( 1, \frac{1}{\chi}; 1 + \frac{1}{\chi}; \frac{-1}{\zeta} \right)}{\Gamma \left( 1 + \frac{1}{\chi} \right) \Gamma \left( 1 - \frac{1}{\chi} \right)} \zeta^k, \quad \zeta > 1. \quad (48) $$

The behaviour at small values of $\zeta$ is read off by picking the term proportional to $\zeta^{1-\chi}$ in the analytic continuation of the hypergeometric function $2F_1$ (see [19], Chapter 15, formula 15.3.7):

$$ 2F_1 \left( 1, \frac{1}{\chi}; 1 + \frac{1}{\chi}; -\frac{1}{\zeta} \right) \sim_{\zeta \to 0} \Gamma \left( 1 + \frac{1}{\chi} \right) \Gamma \left( 1 - \frac{1}{\chi} \right) \zeta^{1-\chi}. \quad (49) $$
At a fixed value of the parameter $\epsilon$, the density therefore goes to infinity as a power of $\zeta^{-1}$ when $\zeta$ goes to zero:

$$\rho(\epsilon, \zeta) \sim_{\zeta \to 0} \frac{\beta_c}{\epsilon} \Gamma \left(1 - \frac{1}{\chi}\right) \Gamma \left(1 + \frac{1}{\chi}\right) \zeta^{\frac{1}{\chi} - 1}. \quad (50)$$

By introducing a smooth test function $\phi$ on $[0, 1]$, we find by dominated convergence that the difference

$$\int_0^1 \phi(x)f(x)dx = -\int_0^1 \frac{\phi(x)dx}{1 + \zeta - f(x)} = \int_0^1 \frac{\phi(1-h)h^\chi}{\zeta + h^\chi}dh \quad (51)$$

has a finite limit when $\zeta$ goes to zero. Hence the singularity of the l.h.s. is the same as that of

$$\int_0^1 \frac{\phi(1-h)}{\zeta + h^\chi} = \frac{1}{\zeta} \, _2F_1 \left(1, \frac{1}{\beta}; 1 + \frac{1}{\beta}; -\frac{1}{\zeta}\right) \phi(1) + \frac{1}{\zeta} \int_0^1 h\phi'(1-h) \, _2F_1 \left(1, \frac{1}{\beta}; 1 + \frac{1}{\beta}; -\frac{h}{\zeta}\right)dh. \quad (52)$$

The factor of $h$ in the integrand in the second term on the r.h.s. implies that this term is less singular than the first one when $\zeta$ goes to zero. An equivalent of this first term is again obtained from Eq. 49. Hence we find a generalisation of the limit of the ratios of average numbers of particles to average density (Eq. 53):

$$\lim_{\zeta \to 0, \text{fixed } \epsilon} \frac{\bar{n}(x)}{\rho(\epsilon, \zeta)} = (\beta_c - \epsilon) \frac{q(x)}{1 - f(x)} + \frac{\epsilon}{\beta_c} \delta_1(x), \quad f(x) \sim_{x \to 1} (1 - x)^\chi, \quad \chi > 1, \quad q(1-h) = O(h^\alpha), \quad \alpha > \chi - 1. \quad (53)$$

The fluctuations can again be expressed using Eq. 41 and the asymptotic expression for the density (Eq. 50), for $f = f_\chi$, with $\chi > 1$:

$$\frac{\Delta n(x)}{n(x)} \sim_{\zeta \to 0} \sqrt{\frac{\epsilon}{\beta_c(\beta_c - \epsilon)}} \zeta^{\frac{\chi - 1}{\chi}} \sim_{\zeta \to 0, \epsilon \to 0} \frac{1}{\beta_c} \sqrt{\frac{\epsilon}{\Gamma \left(1 - \frac{1}{\chi}\right) \Gamma \left(1 + \frac{1}{\chi}\right) q(x)}} \zeta^{\frac{\chi - 1}{\chi}}. \quad (54)$$

8 Summary and discussion

We have studied the steady states of a non-conserving zero-range process with extensive hopping, creation and annihilation rates, on a fully connected lattice with a large number of sites. This model can naturally be interpreted as a stochastic model of the balance between selection and mutation. Site labels model the bounded fitness. Site-dependent creation rates model selection, and the hopping process with extensive rates models the introduction of new mutants. Assuming that the probability of each configuration factorises (which is a mean-field approximation and is reasonable since the lattice is fully connected), we established that the number of particles at each site is distributed according to a negative binomial law, with site-dependent parameters. The average density of the system can be expressed in the steady state in terms of integrals of the mutant density and selection function. The average population at each fitness level in $[0, 1]$ is dominated at large density by a skewed version of the mutant density.

In the limit of large density, the relative fluctuation of the population at each fitness level in $[0, 1]$ goes to zero. The limit of large density is controlled by the parameter we denoted by $\zeta$, which
must be positive for a steady state to be reached, and equals $\beta + \delta - 1$, where $\beta$ is the mutation rate and $\delta$ is the annihilation rate. The inverse of $\zeta$ equals the average number of individual at the maximum fitness level. The rate of divergence of the average density of the system (when the parameter $\zeta$ goes to zero) has been found to depend only on the local behaviour of the selection function at maximal fitness.

In the region of the $(\beta, \delta)$ plane close to the half-line of equation $\beta + \delta = 1$, $\beta < \beta_c$, a non-conserving ZRP with extensive hopping rate exhibits a macroscopically large number of particles in the level of highest fitness, whereas condensation in the conserving ZRP is known to occur only for decreasing hopping functions. Moreover, the expression of the critical value $\beta_c$ is identical as the one worked out in the house-of-cards model.

Considering the entire population with random evolution processes (with ancestors contributing to the distribution of fitness until they die), is more realistic than the approach of the house-of-cards model in which each individual is assigned a generation label. Moreover, the present approach allows for an explicit estimate of the density of the population even if the case of non-linear selection function $f$. It has been appreciated that the local behaviour of $q$ at maximum fitness value is responsible for the emergence of condensation [15], but the derivations rely strongly on the distribution of the moments of the distributions $p_n$ and $q$ at all orders. These moments emerge naturally from the normalisation of the measure process (Eq. 2). The mean-field approach makes use of the thermodynamic limit in two ways: through the large number of sites $L$, which allows to take the continuum limit of the values of fitness, and through the large average number of particles in the system, that controls the fluctuations of the population at each level of fitness.

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