# Stochastic competition between two populations in space

Simone Pigolotti[1], Roberto Benzi[2], Mogens H. Jensen[3], Prasad Perlekar[4], and Federico Toschi[5]

[1] Dept. de Fisica i Eng. Nuclear, Universitat Politecnica de Catalunya Edif. GAIA, Rambla Sant Nebridi s/n, 08222 Terrassa, Barcelona, Spain.

[2] Dipartimento di Fisica, Universita' di Roma "Tor Vergata" and INFN, via della Ricerca Scientifica 1, 00133 Roma, Italy.

[3] The Niels Bohr Institut, University of Copenhagen, Blegdamsvej 17, DD-2100 Copenhagen, Denmark.

[4] Tata Institute of Fundamental Research, Centre for Interdisciplinary Sciences, 21 Brundavan Colony, Narsingi, Hyderabad 500075, India

[5] Department of Physics, Department of Mathematics and Computer Science, and J.M. Burgerscentrum, Eindhoven University of Technology, 5600 MB Eindhoven, The Netherlands and CNR-IAC, Via dei Taurini 19, 00185 Rome, Italy.

**Abstract** We present a model describing spatial competition between two biological populations. Individuals belonging to the two populations diffuse in space, reproduce, and die as effect of competitions; all these processes are implemented stochastically. We focus on how the macroscopic equations for the densities of the two species can be derived within the formalism of the chemical master equations. We also compare the case in which the total density of individuals is kept fixed by constraint with a case in which it can fluctuate.

## 1 Introduction

Competition between biological populations can be mathematically described at different levels of complexity. For example, when spatial degrees of freedom and number fluctuations are neglected, competition models are relatively easy to analyze with tools of dynamical system theory. A paradigmatic example of this case are Lotka-Volterra models, see e.g. (Murray, 2007).

However, in many biological situations, the spatial distribution of the populations cannot be neglected, so that one is forced to consider spatially

A. Muntean, F. Toschi (Eds.), *Collective Dynamics from Bacteria to Crowds*, CISM International Centre for Mechanical Sciences, DOI 10.1007/978-3-7091-1785-9_4, 

explicit models. Moreover, stochasticity can be also important. This is especially the case in neutral or near-neutral conditions, where the parameters characterizing the species are the same (or nearly), and the outcome of competition is determined by chance rather than by fitness differences.

In this chapter, we analyze two spatial competition models. The first is the stepping stone model, originally introduced by Kimura (Kimura, 1953; Kimura and Weiss, 1964). A key assumption of the stepping stone model is that the sum of the number of individuals belonging to the two species is kept constant at each point in space; this assumption is relaxed in the second model (Pigolotti et al., 2012, 2013). For both models, we show how one can generally derive the macroscopic dynamic equations describing the concentrations of the two species using the formalism of the chemical master equation (see e.g. Gardiner (2004), chapter 8), which can be thought of as a generalization of the Kramers-Moyal expansion for spatially extended systems. After presenting this derivation and discussing its limits of validity for the two models, we show some analytical and numerical results in the case in which the two species are neutral, i.e. characterized by the same rates.

## 2 The Stepping Stone Model

The stepping stone model (Kimura, 1953; Kimura and Weiss, 1964) is a paradigmatic model for spatial population genetics. Let us consider a system made up of different islands (or "demes"), each hosting two populations, $A$ and $B$. The total population of each island is a fixed parameter $N_l$. We denote with $n$ the population of species $A$, so that the population of species $B$ is $N_l - n$. The two populations undergo a Moran process: at a given rate, an individual is chosen at random, killed and replaced with a copy of one of the other individuals on the island, also chosen at random. To model the possibility of a selective advantage, individuals of space $A$ are copied with a rate $\mu(1+s)$, while individuals of species $B$ are copied at a rate $\mu$. The parameter $\mu$ can be interpreted as an inverse generation time, while $s$ represents the relative selective advantage of species $A$. The rates at which population $A$ increases or decreases are then given by:

$$\begin{aligned} W^+(n_i) &= (1+s)\mu \frac{N_l - n_i}{N_l}\frac{n_i}{N_l} \\ W^-(n_i) &= \mu \frac{n_i}{N_l}\frac{N_l - n_i}{N_l}. \end{aligned} \tag{1}$$

For simplicity, we first discuss the well-mixed version of the model, i.e.

the dynamics on a single island, which reduces to the well-known Moran model. In the second part of this section, we will describe the one dimensional case of a linear array made up of many islands, where the rates above will be complemented by immigration/emigration rates between neighboring islands.

The definition of the rates in (1) directly leads to the following master equation

$$\frac{d}{dt}P(n_i,t) = W^+(n_{i-1})P(n_{i-1},t) + \\ +W^+(n_{i+1})P(n_{i+1},t) - [W^+(n_i) + W^-(n_i)]P(n_i,t). \tag{2}$$

The next step consists in approximating the birth-death process defined above into a Langevin equation by means of a Kramers-Moyal expansion. Formally, the master equation (2) can be written in an integral form as

$$\frac{d}{dt}P(n,t) = \int d(\Delta n)[\omega(\Delta n, n-\Delta n)P(n-\Delta n) - \omega(\Delta n, n)P(n)] \tag{3}$$

where the jump rates have been incorporated into a jump distribution function $\omega$:

$$\omega(\delta n, n) = \delta(\Delta n - 1)W^+(n) + \delta(\Delta n + 1)W^-(n). \tag{4}$$

The trick is now to perform a Taylor expansion of Eq. (3) around $\Delta n = 0$, leading to

$$\frac{d}{dt}P(n,t) = \sum_{j=1}^{\infty} \frac{(-1)^j}{j!}\frac{d^j}{dn^j}[\alpha_j(n)P(n,t)] \tag{5}$$

where the $\alpha_j$'s are the moments of the jump distribution,

$$\alpha_j(n) = \int d(\Delta n)(\Delta n)^j \omega(\Delta n, n). \tag{6}$$

Assuming $N_l \gg 1$, we can introduce the new variable $f = n/N_l$. The quantity $f$ can be interpreted as the fraction of one species: $f = 1$ means an island exclusively populated with one allele and $f = 0$ means exclusive occupation by the alternative genotype. The jumps in terms of the new variable $\delta f = \pm 1/N_l$ are now small, so that we can truncate the above expansion up to the second derivative. This yields a Fokker-Planck equation:

$$\partial_t P(f,t) = -\partial_f[\mu s f(1-f)P(f,t)] + \partial_f^2\left[\frac{\mu f(1-f)}{N_l}P(f,t)\right] \tag{7}$$

where we neglected terms of order $s/N$ by assuming $N \gg 1$ and $s \gg 1$. The corresponding Langevin equation is

$$\partial_t f(t) = \mu s f(1-f) + \sqrt{\frac{2\mu f(1-f)}{N_l}}\xi(t) \tag{8}$$

where $\xi(\mathbf{x}, t)$ is a Gaussian stochastic process, delta-correlated in time, $\langle \xi(t)\xi(t')\rangle = \delta(t-t')$. The nonlinearity multiplying the noise requires an interpretation in terms of the Ito calculus; this will also be the case for all generalizations we will consider in the following.

We now move to the one-dimensional case. We consider an infinite linear array of islands (or "demes"), where two neighboring islands are separated by a distance $a$. Each island host a total population $N_l$ of individuals belonging to the two species $A$ and $B$. Numbering the islands with an index $i$, we denote with $n_i$ the population of species $A$ in the island $i$, so that the population of species $B$ will be $N_l - n_i$. The local dynamics on each island is the same as before; the only additional ingredient is that we allow neighboring island for exchanging individuals. It is convenient to call the exchange rate from an island to a neighboring one as $DN/a^2$, where $D$ is an additional free parameter. We can proceed as before by performing a Kramers-Moyal expansion in each island and introducing the local fractions $f_i = n_i/N_l$. The result is a set of Langevin equations:

$$\partial_t f_i(\mathbf{x}, t) = \frac{D}{2a^2}(f_{i-1} + f_{i+1} - 2f_i) + \mu s f_i(1-f_i) + \sqrt{\frac{2\mu f_i(1-f_i)}{N_l}}\xi_i(t) \tag{9}$$

where noise sources corresponding to different islands are uncorrelated. It is now possible to (formally) take the continuum limit $a \to 0$, leading to

$$\partial_t f(\mathbf{x}, t) = D\nabla^2 f(\mathbf{x}, t) + \mu s f(1-f) + \sqrt{\frac{2\mu f(1-f)}{N}}\xi(\mathbf{x}, t) \tag{10}$$

where $N = N_l/a$: it is convenient to distinguish between $N_l$ (the population inside a single discrete deme of the SSM) and $N$ (the corresponding total density of individuals). Notice that $N_l$ is a non-dimensional quantity, while $N$ is a density, carrying units of an inverse length. In the above equation, $\xi(\mathbf{x}, t)$ is a Gaussian stochastic process, delta correlated in space and time, $\langle \xi(\mathbf{x}, t)\xi(\mathbf{x}', t')\rangle = \delta(\mathbf{x} - \mathbf{x}')\delta(t - t')$.

We conclude with a few remarks about the validity of this continuous limit. Equations (7) and (8) have been derived by means of the Kramers-Moyal equation, which strictly speaking is not a systematic expansion in

a small parameters. However, the same equation can be more rigorously derived in the framework of Van Kampen's system size expansion, where the expansion parameter is $1/N_l$ (see e.g. Risken (1989); Gardiner (2004) for a discussion of this problem). The continuum limit of Eq. (10) should be considered as a short notation, as the system size expansion is valid only when the local population size $N_l = Na$ is large; this assumption clearly breaks down in the limit of $a \to 0$, see (Law et al., 2003; Doering et al., 2003; Hernandez-Garcia and Lopez, 2004; Birch and Young, 2006; Pigolotti et al., 2013) for examples in which this assumption is violated.

## 3 Model without total density conservation

We consider individuals as diffusing particles in $d$ dimensions. We implement population dynamics by assuming that individuals of species $i$ reproduce at rate $\mu_i$ and die with rates $\tilde{\lambda}_{ij}$ proportional to the number of individuals of species $j$ in a given neighborhood. In a language borrowed from chemical kinetics, the "reactions" we consider are:

$$\begin{aligned} X_i &\xrightarrow{\mu_i} 2X_i \qquad \text{(reproduction)} \\ X_i + X_j &\xrightarrow{\tilde{\lambda}_{ij}} X_i \qquad \text{(death by competition)} \end{aligned} \tag{11}$$

In particular, competition occurs when individuals are within a small volume $\delta$ (for details on the numerical implementation of the individual-based dynamics see Perlekar et al. (2011)). We can then discretize the system in cells of size $\delta$ and start the derivation from the master equation governing the time evolution of the probability the numbers of particles $\{n_j^A, n_j^B\}$ of type $A$ and $B$ in each cell, labeled by the index $j$. We first define the rates $W_A(\pm 1, n_j^A, n_j^B)$ and $W_B(\pm 1, n_j^A, n_j^B)$ at which the populations of type $A$ (or $B$) increase/decrease by one individual in a specific box, given that the population sizes are $n_j^A$ and $n_j^B$. Letting aside the diffusion terms, the expression for these rates are:

$$\begin{aligned} W_A(+1, n_j^A, n_j^B) &= \mu_A n_j^A \\ W_A(-1, n_j^A, n_j^B) &= \tilde{\lambda}_{AA} n_j^A (n_j^A - 1) + \tilde{\lambda}_{AB} n_j^A n_j^B \\ W_B(+1, n_j^A, n_j^B) &= \mu_A n_j^B \\ W_B(-1, n_j^A, n_j^B) &= \tilde{\lambda}_{BA} n_j^A n_j^B + \tilde{\lambda}_{BB} n_j^B (n_j^B - 1). \end{aligned} \tag{12}$$

The master equation governing the evolution of the full probability distribution $P(\{n_j^A, n_j^B\}, t)$ for all possible box occupation numbers $\{n_j^A, n_j^B\}$

then reads:

$$\begin{aligned}
\tfrac{d}{dt} \quad & P(\{n_j^A, n_j^B\}, t) = \\
= \quad & \sum_j [W_A(+1, n_j^A - 1, n_j^B) P(n_1^A, \ldots, n_j^A - 1, \ldots, n_1^B, \ldots) \\
- \quad & W_A(+1, n_j^A, n_j^B) P(\{n_j^A, n_j^B\})] \\
+ \quad & \sum_j [W_A(-1, n_j^A + 1, n_j^B) P(n_1^A, \ldots, n_j^A + 1, \ldots, n_1^B, \ldots) \\
- \quad & W_A(-1, n_j^A, n_j^B) P(\{n_j^A, n_j^B\})] \\
+ \quad & \sum_j [W_B(+1, n_j^A, n_j^B - 1) P(n_1^A, \ldots, n_1^B, \ldots, n_j^B - 1, \ldots) \\
- \quad & W_B(+1, n_j^A, n_j^B) P(\{n_j^A, n_j^B\})] \\
+ \quad & \sum_j [W_B(-1, n_j^A, n_j^B + 1) P(n_1^A, \ldots, n_1^B, \ldots, n_j^B + 1, \ldots) \\
- \quad & W_B(-1, n_j^A, n_j^B) P(\{n_j^A, n_j^B\})] \\
+ \quad & \text{diffusion terms,}
\end{aligned} \tag{13}$$

where the diffusion terms account for the stochastic exchange of particles between neighboring boxes. As in the case of the stepping stone model, these terms reduce to discrete approximations to Laplace operator. Indeed, we will replace them with Laplacians in the continuous space limit at the end of the calculation.

In analogy with the previous section, we now to perform a Kramers-Moyal expansion (Risken, 1989) in each of the boxes. The only difference is that in this case it is a two-variable system, so we have to expand in the two independent increments $\Delta n_A$ and $\Delta n_B$. The result is

$$\begin{aligned}
\partial_t P\{n_j^A, n_j^B\} \quad = \quad & \sum_j \sum_{k=1}^{\infty} \frac{(-1)^k}{k!} \{\partial_{n_j^A}^k [\alpha_k^A(n_j^A, n_j^B) P(\{n_j^A, n_j^B\})] + \\
+ \quad & \partial_{n_j^B}^k [\alpha_k^B(n_j^A, n_j^B) P(\{n_j^A, n_j^B\})]\},
\end{aligned} \tag{14}$$

with the moments of the two jump distribution functions defined by

$$\alpha_k^{A,B}(n_j^A, n_j^B) = \int d\Delta n_j^{A,B} \; (\Delta n_j^{A,B})^k \omega^{A,B}(\Delta n_j^{A,B}, n, j^A, n_j^B) \tag{15}$$

and the function $\omega$ is defined from the rates exactly as in the previous section. Finally, truncating the Kramers-Moyal expansion up to second order in the derivatives leads to a Fokker-Planck equation for $P\{n_j^A, n_j^B\}$. It

is convenient to write directly the equivalent but somewhat simpler system of Langevin equations corresponding to this Fokker-Planck description, namely:

$$\begin{aligned}\frac{dn_j^A}{dt} &= n_j^A(\mu_A - \tilde{\lambda}_{AA}n_j^A - \tilde{\lambda}_{AB}n_j^B) + \text{diffusion} + \sigma_{A,j}\xi_j^A \\ \frac{dn_j^B}{dt} &= n_j^B(\mu_B - \tilde{\lambda}_{BA}n_j^A - \tilde{\lambda}_{BB}n_j^B) + \text{diffusion} + \sigma_{B,j}\xi_j^B \end{aligned} \tag{16}$$

where the noise amplitudes are

$$\begin{aligned}\sigma_{A,j}^2 &= n_j^A(\mu_A + \tilde{\lambda}_{AA}n_j^A + \tilde{\lambda}_{AB}n_j^B) \\ \sigma_{B,j}^2 &= n_j^B(\mu_B + \tilde{\lambda}_{BA}n_j^A + \tilde{\lambda}_{BB}n_j^B). \end{aligned} \tag{17}$$

In Eqns. (16), the $\xi$'s are delta-correlated unit variance Gaussian processes, $< \xi_j^k(t)\xi_l^m(t') >= \delta_{jl}\delta_{km}\delta(t-t')$. In principle, the diffusion terms in (13) would contribute to the noise term. However, one can show that this contribution can be neglected if the size of the cells is sufficiently large (see Gardiner (2004)). In analogy with the previous section, from Eqs.(16) one can take (formally) the limit $\delta \to 0$. In such a way the number densities of individuals become continuous functions of the coordinate $\mathbf{x}$, $n_A(\mathbf{x},t)$ and $n_B(\mathbf{x},t)$.

We also define rescaled, macroscopic rates of binary reactions, $\lambda_{ij} = N\delta\tilde{\lambda}_{ij}$, and the macroscopic concentrations of individuals

$$c_{A,B}(\mathbf{x},t) = n_{A,B}(\mathbf{x},t)/N.$$

It is convenient to perform this rescaling in a different way for the well-mixed case (in which the population is not structured in space) and for the one dimensional case. In the former case we take $\delta = 1$. In analogy with the stepping stone model, calling $N_l = \delta N$ the local population size, we simply have $N = N_l$. In the spatial case, we fix $\delta = 1/N$ so that $\lambda_{ij} = \tilde{\lambda}_{ij}$, $\forall i,j$. This procedure leads to the following coupled spatial Langevin equations

$$\begin{aligned}\frac{\partial}{\partial t}c_A &= D\nabla^2 c_A + c_A(\mu_A - \lambda_{AA}c_A - \lambda_{AB}c_B) + \sigma_A\xi \\ \frac{\partial}{\partial t}c_B &= D\nabla^2 c_B + c_B(\mu_B - \lambda_{BA}c_A - \lambda_{BB}c_B) + \sigma_B\xi' \end{aligned} \tag{18}$$

where

$$\begin{aligned}\sigma_A^2 &= \frac{c_A(\mu_A + \lambda_{AA}c_A + \lambda_{AB}c_B)}{N} \\ \sigma_B^2 &= \frac{c_B(\mu_B + \lambda_{BA}c_A + \lambda_{BB}c_B)}{N}. \end{aligned} \tag{19}$$

## 4 Neutral theory

In this section, we present results in the simple case

$$\mu_A = \mu_B = \lambda_{AA} = \lambda_{AB} = \lambda_{BA} = \lambda_{BB}. \tag{20}$$

This case represent the neutral situation in which the two variants are neutral, i.e. phenotypically equivalent.

As before, we start our discussion with the well-mixed case. It is useful to describe the dynamics of the neutral version of the model in the $c_A$ vs. $c_B$ plane, represented in Fig. (1, left). Starting from a dilute initial condition, the system evolves rapidly towards to the intrinsic overall carrying capacity given by $c_A + c_B = 1$. The dynamics is then localized with fluctuations near this line, until extinction of one of the two species. This contrasts with the Moran process, in which the dynamics is rigidly confined to the $c_A + c_B = 1$ line. To assess the effect of these fluctuations, note from Eq. (18) that in the neutral case the total concentration $c_T = c_A + c_B$ obeys a closed equation:

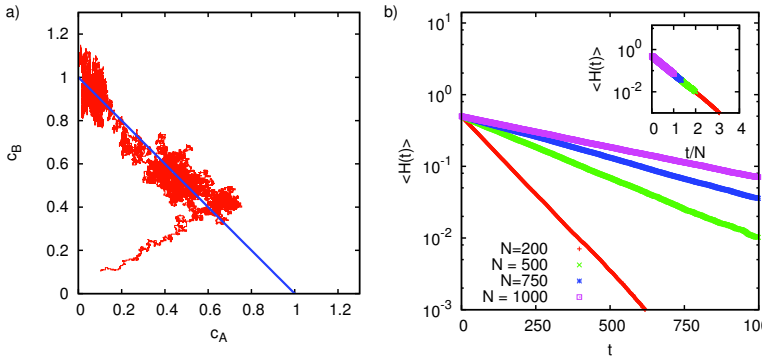


**Figure 1.** Neutral dynamics in the well-mixed case. (a) Example of a trajectory in the $(c_A, c_B)$ plane with $N = 500$. The initial condition is $n_A = n_B = 20$, i.e. a small fraction of a typical long time carrying capacity. (b) Decay of the average heterozygosity $\langle H(t) \rangle$ for different values of $N$. Curves are obtained from simulations of the particle model; each curve is an average over $10^4$ realizations and the error bars are smaller than the size of the lines. (inset) Collapse of the same curves plotted as a function of $t/N$. From Pigolotti et al. (2013).

$$\frac{d}{dt} c_T = \mu c_T (1 - c_T) + \sqrt{\frac{\mu c_T (1 + c_T)}{N}} \xi_c, \tag{21}$$

decoupled from the fraction of species $A$, $f = c_A/(c_A + c_B)$, where the noise term $\xi_c$ satisfies $\langle \xi_c(t)\xi_c(t')\rangle = \delta(t-t')$. When $N$ is large, the stationary solution, beside the solution $P(c) = \delta(c)$ corresponding to global extinction, is approximately a Gaussian with average $\langle c_T\rangle = 1$ and variance $\langle c_T^2\rangle - \langle c_T\rangle^2 = N^{-1}$, which is small when $N$ is large. We remind that, as in the particle model for simplicity death is implemented only via binary reactions (see Eq. 12), the state of global extinction is not accessible in the particle model, while it constitutes an absorbing state for Eq. 21. Such discrepancy with the macroscopic equation could be easily removed by allowing for death even in absence of competition, i.e. the reaction $X_i \to \emptyset$.

We now describe the dynamics of the relative fraction $f$ of individuals carrying allele $A$, $f(t) = c_A/(c_A + c_B)$. Let us recall Ito's formula for a two variable system: let us write the Langevin equations for the two densities $c_A$ and $c_B$ as

$$\begin{aligned} \frac{d}{dt}c_A(\mathbf{x},t) &= \alpha_A(c_A,c_B) + \sigma_A(c_A,c_B)\xi(\mathbf{x},t) \\ \frac{d}{dt}c_B(\mathbf{x},t) &= \alpha_B(c_A,c_B) + \sigma_B(c_A,c_B)\xi'(\mathbf{x},t) \end{aligned} \tag{22}$$

where the diffusive Laplacian terms are included into $\alpha_A$, $\alpha_B$. The equation for $f(t)$ then reads

$$\begin{aligned} \frac{d}{dt}f &= \alpha_A\partial_A f + \alpha_B\partial_B f + \sqrt{\sigma_A^2(\partial_A f)^2 + \sigma_B^2(\partial_B f)^2}\xi + \\ &+ \frac{\sigma_A^2}{2}\partial_{AA}f + \frac{\sigma_B^2}{2}\partial_{BB}f, \end{aligned} \tag{23}$$

where we used the abbreviated notation $\partial_A \equiv \partial_{c_A}$, $\partial_{AA} \equiv \partial^2_{c_A}$ and so on. Inserting the complete set of equations (18) into (23) leads to a lengthy expression for the dynamics of $f$. However, with the simple neutral choice of the parameters presented above in (20), the equation reduces to

$$\frac{d}{dt}f = \sqrt{\mu f(1-f)\frac{1+c_T}{Nc_T}}\xi_f \tag{24}$$

where $\xi_f(t)$ also satisfies $\langle \xi_f(t)\xi_f(t')\rangle = \delta(t-t')$, and further we have $\langle \xi_f(t)\xi_c(t')\rangle = 0$. The above equation is the same as the equation for the stepping stone model, Eq. (8), in the neutral case $s = 0$, apart from the coupling with the total density $c_T$ which evolves dynamically according to (21). We can now analyze the global heterozygosity, which quantifies the loss of diversity as time evolves and is defined as the probability $H(t) = 2\langle f(1-f)\rangle$

that two randomly chosen individuals in the population carry different alleles. As the equation for $c_T$ is independent of $f$ in the neutral case studied here, one can factorize the average over $c_T$ and $f$ in the equation for $H(t)$:

$$\begin{aligned} \frac{d}{dt}H(t) &= -\frac{\mu}{N}\left\langle f(1-f)\frac{1+c_T}{c_T}\right\rangle = -\frac{\mu}{N}\left\langle f(1-f)\right\rangle \left\langle \frac{1+c_T}{c_T}\right\rangle \\ &= -\frac{2\mu}{N}H(t) + O\left(\frac{1}{N^2}\right). \end{aligned} \tag{25}$$

Neglecting the correction of order $N^{-2}$, we recover for our model with density fluctuations the closed equation for $H(t)$ for Fisher-Wright and Moran-type models with a fixed population size derived by Kimura, which states that the total heterozygosity decays exponentially in well mixed neutral systems (Crow and Kimura, 1970):

$$\langle H(t)\rangle = H(0)\exp(-2\mu t/N) \tag{26}$$

This exponential behavior is confirmed in simulations, as shown in Fig. (1b).

We now move to the one and two dimensional cases. To study how fixation occurs in space, we study the behavior of the *spatial* heterozygosity $H(x,t)$ defined as the probability of two individuals at distance $x$ and time $t$ to carry different alleles. In the neutral stepping stone model with a fixed population size in each deme, $H(x,t)$ obeys a closed equation:

$$\partial_t H(x,t) = 2D\nabla^2 H - \frac{2\mu}{N}H\delta(x). \tag{27}$$

In one dimension, such equation can be solved explicitly:

$$H(x,t) = H_0\left[1 - \frac{2}{N}\int_0^t dt' \frac{\mathrm{erf}\left(\frac{t'}{4N^2D}\right)}{\sqrt{8\pi D(t-t')}} e^{-\frac{x^2}{8D(t-t')}+\frac{t'}{4N^2D}}\right] \tag{28}$$

where $H_0$ is the initial heterozygosity, equal to one half if the two variants are well mixed and equally populated at time $t = 0$. Eqs. (27) and (28) can be derived directly from the stochastic Fisher equation (10) with $s = 0$ (see, e.g., Korolev et al. (2009)).

We define the heterozygosity in the off-lattice particle simulations with growth and competition from the statistics of interparticle distances. In particular, at a given time $t$, we compute all distances between pairs of individuals. Upon introducing a bin size $h$, the function $H(r,t)$ is then

defined as the ratio between the number of pairs carrying *different* alleles at a separation between $r$ and $r + h$, divided by the total number of pairs of all types in the same range of separation. For simplicity, we always took the bin size $h$ equal to the interaction distance $\delta$.

In the limit $N\sqrt{D/\mu} \gg 1$, the spatial heterozygosity obtained by simulations of the neutral off-lattice model shows a remarkable agreement with Eq. (28), as shown in Fig. (2). This correspondence arises because, also in the spatial case, the relative fraction of allele $A$, $f(x,t) = c_A/(c_A + c_B)$, obeys a very similar equations as discussed in the mean field case. By applying Ito's formula in the spatial case as before, one can show that the only difference is an additional effective advection term in the equation for $\partial_t f$, equal to $2D(\nabla \log c_T) \cdot \nabla f$. The appearance of such terms was firstly found in Vlad et al. (2004) in a deterministic version of the model described here. Since $c_T$ obeys a decoupled equation in the neutral case, such terms do not affect the equation for the heterozygosity. Indeed, numerical simulation shows that the average spatial heterozygosity in the model reproduces that of the stepping stone model even in the limit of very high diffusivity, as shown in Fig. 2, panel (b). Panel (c) shows that similar agreements arise comparing numerical integration of Eq. (27) with our off-lattice simulations in two dimensions. At variance with the one dimensional case, where the local heterozygosity $H(0,t)$ decays at long times as $t^{-1/2}$, in two dimension the decay is much slower, $H(0,t) \sim 1/\ln(t)$. Such slow logarithmic decay is confirmed in simulations in panel (d).

## 5 Conclusions

In this Chapter we compared two different stochastic models of spatially extended populations. We have shown that one can formally demonstrate their equivalence by means of stochastic calculus, at least in the case of neutral species. While the stepping stone model allows for a simpler analysis, the more general model is appropriate for cases in which the total density of individuals can vary considerably due to external causes, as a non-homogeneous distribution of resources or transport by fluid flows (Pigolotti et al., 2012, 2013).

## Bibliography

D. A. Birch and W. A Young. A master equation for a spatial population model with pair interactions. *Theo. Pop. Biol.*, 70(1):2642, 2006.

J.F. Crow and M. Kimura. *Introduction to Population Genetics Theory.* Harper & Row Publishers, 1970.

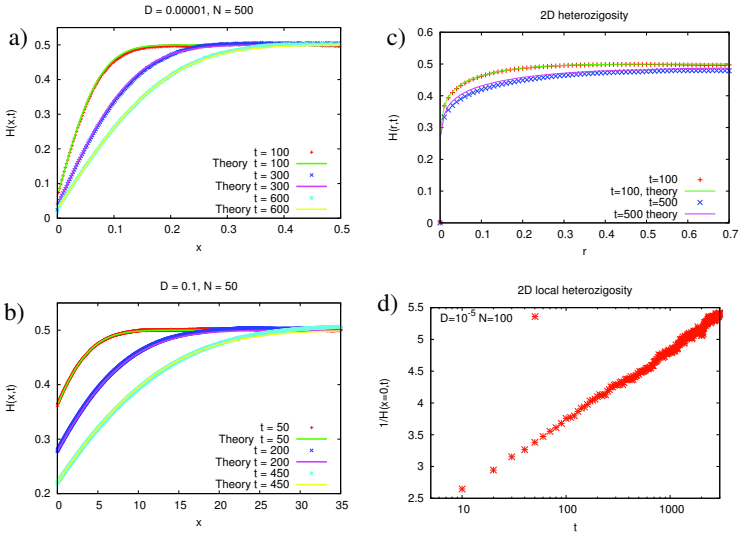


**Figure 2.** Heterozygosity in the $1d$ and $2d$ neutral case. Behavior of heterozygosity correlation function for the neutral off-lattice model of growth and competition. (a) 1D simulations at low diffusivity, $D = 10^{-5}$ and (b) high diffusivity, $D = 0.1$. In the top case, the system size is $L = 1$ while in the bottom case the system size is $L = 100$. In both cases we find excellent agreement with the prediction of formula (28). (c) Neutral heterozygosity in $2d$, compared with a numerical integration of Eq. (27). (d) Behavior of the local heterozygosity $H(x = 0, t)$ as a function of time in 2D, showing the logarithmic decay $H(x = 0, t) \sim 1/\ln(t)$. From Pigolotti et al. (2013).

C. Doering, C. Mueller, and P. Smereka. Interacting particles, the stochastic fkpp equation, and duality. *Physica A*, 325:243–259, 2003.

C.W. Gardiner. *Handbook of Stochastic Methods*. Springer, 2004.

E. Hernandez-Garcia and C. Lopez. Clustering, advection and patterns in a model of population dynamics with neighborhood-dependent rates. *Phys. Rev. E*, 70(1):016216, 2004.

M. Kimura. "stepping stone" model of population. *Ann. Rept. Nat. Inst. Genetics*, 3:62–63, 1953.

M. Kimura and G. H. Weiss. The stepping stone model of population structure and the decrease of genetic correlation with distance. *Genetics*, 49: 561–576, 1964.

K.S. Korolev, M. Avlund, O. Hallatschek, and D.R. Nelson. Genetic demixing and evolutionary forces in the one-dimensional stepping stone model. *Review of Modern Physics*, 82:1691–1718, 2009.

R. Law, D. J. Murrell, and U. Dieckmann. Population growth in space and time: the spatial logistic equation. *Ecology*, 84(1):252–262, 2003.

J. D. Murray. *Mathematical Biology: an Introduction*. Springer, 2007.

P. Perlekar, R. Benzi, S. Pigolotti, and F. Toschi. Particle algorithms for population dynamics in flows. *Journal of Physics: Conference Series*, 333:012013, 2011.

S. Pigolotti, R. Benzi, M.H. Jensen, and D.R. Nelson. Population genetics in compressible flows. *Physical Review Letters*, 108:128102, 2012.

S. Pigolotti, R. Benzi, P. Perlekar, M.H. Jensen, F. Toschi, and D.R. Nelson. Growth, competition and cooperation in spatial population genetics. *Theoretical Population Biology*, 84:72–86, 2013.

H. Risken. *The Fokker-Planck equation: Methods of Solution and Applications*. Springer, Berlin, 1989.

M. Vlad, L. L. Cavalli-Sforza, and J. Ross. Enhanced (hydrodynamic) transport induced by population growth in reaction-diffusion systems with application to population genetics. *Proceedings of the National Academy of Sciences of the United States of America*, 101(28):10249–10253, 2004.