Supporting information: Bet-hedging strategies in expanding populations

Paula Villa Martín

Biological Complexity Unit, Okinawa Institute of Science and Technology Graduate University, Onna, Okinawa 904-0495, Japan

Miguel A. Muñoz

Departamento de Electromagnetismo y Física de la Materia and Instituto Carlos I de Física Teórica y Computacional, Facultad de Ciencias, Universidad de Granada, 18071 Granada, Spain

Simone Pigolotti*

Biological Complexity Unit, Okinawa Institute of Science and Technology Graduate University, Onna, Okinawa 904-0495, Japan. (Dated: April 2, 2019)

NUMERICAL INTEGRATION OF THE STOCHASTIC FISHER EQUATION

In this section we describe in details the methods for the integration of the wave equations of the two-phenotype model used for simulations in the Main Text.

Fisher wave

We consider the Fisher equation

$$\dot{f}(x,t) = D\nabla^2 f(x,t) + \sigma(x,t)f(x,t)(1 - f(x,t)),$$
(1)

where f(x,t) is the population density at space x and time t, and $\sigma(x,t)$ is the local growth rate.

We employ a finite-difference fourth-order Runge-Kutta method. The systems is initialized by fixing $f(x_i, 0) = 1$ for $i \in (0, 50)$ and f(x, t) = 0 for i > 50. The spatial mesh dx is fixed by means of an adaptive routine. We initialize the routine with an initial guess dx = 0.14. Then

- 1. We let the system evolve until the front reaches a stationary state.
- 2. We compute the smallest values of x for which $f(x,t) > \theta$ for $\theta = 3/4$ and $\theta = 1/4$. We denote these two values as $x_{3/4}$ and $x_{1/4}$ respectively.
- 3. We measure the precisions $\Delta f_{3/4} = f(x_{3/4} dx) f(x_{3/4}), \ \Delta f_{1/4} = f(x_{1/4} dx) f(x_{1/4}).$
- 4. If $\Delta f_{3/4} > 0.01$ and $\Delta f_{1/4} > 0.01$, then dx is accepted as a valid increment.
- 5. Otherwise, the system is reset to the initial condition and the routine is again run for $dx = d\tilde{x} 0.01$; being $d\tilde{x}$ the previous spatial mesh.

Once dx is determined, dt is fixed following the Courant-Friedrichs-Lewy condition for an explicit integration method [1]:

$$\frac{v_{\max}dt}{dx} \le 1 \tag{2}$$

* simone.pigolotti@oist.jp

being v_{max} the estimated maximum velocity of the wave. We fix $v_{\text{max}} = 100$, which is sufficiently large compared to velocities in our simulations.

Temporal environmental switch is numerically implemented with a simple first-order algorithm. At the beginning of each time step, the state of environment is switched with probability k dt. We verified that this quantity is always sufficiently small, so that the first-order algorithm yields reliable results. A similar algorithm is implemented for spatial environmental variations to sequentially assign an environmental state to each lattice site.

Stochastic Fisher wave

We consider the stochastic Fisher equation [2]

$$\dot{f}(x,t) = D\nabla^2 f + \sigma(t)f(1-f) + \sqrt{\frac{2}{N}f(1-f)}\xi(x,t)$$
(3)

where $\xi(x,t)$ a Gaussian white noise satisfying $\langle \xi(x,t) \rangle = 0$ and $\langle \xi(x,t)\xi(x',t') \rangle = \delta(x-x')\delta(t-t')$. For later convenience, we define the noise amplitude $\gamma(t) \equiv \sqrt{\frac{2}{N}f(t)(1-f(t))}$.

Numerical integration in the presence of noise is subtle. In particular, one has to figure out how to deal with the unphysical values f(x,t) < 0 and f(x,t) > 1 that can result due to finite numerical precision. Depending on parameter range, the naive replacement f(x,t) = 0 or f(x,t) = 1 when f(x,t) < 0 and f(x,t) > 1, respectively, may introduce a substantial bias. In particular, an incorrect integration of f(x,t) at the front, where f(x,t) is small, might lead to an large error in the estimated velocity. However, when f(x,t) is small so that $\gamma(t) \simeq \sqrt{\frac{2}{N}f(t)}$, this problem can be circumvented by integrating the noise term exactly [3], while integrating the rest of the equation deterministically [4].



FIG. 1. Size scaling and maximum error estimation for our integration method. Panel A) shows the curve $4.5 (\log N)^{-2}$ and the difference $v_F - v$ for k = 0, $\alpha = 0$, $s_s = 1$, and different system sizes. Panel B) shows $(v_F - v)/v_F$ for $N = 10^9$ and different growth rates employed in this work. These results suggest that our integration method is precise and have a maximum error of 0.0018%.

We follow this strategy and integrate the equation mixing two different algorithms, depending on the local value of f(x, t):

• If $f(x,t) > \theta$: we employ the Milstein method (order 1). Defining $\beta(t) \equiv D\nabla^2 f(t) + \sigma(t)f(t)(1-f(t))$, the local field is updated according to the rule

$$f(x,t+dt) = f(x,t) + \beta(t)dt + \gamma(t)\Delta + \frac{1}{2}\gamma(t)\frac{\partial\gamma}{\partial f(t)}(\Delta^2 - dt)$$
(4)

being $\Delta = \sqrt{dt}g(t)$, where g(t) is a Gaussian random variable with zero mean and unit variance, drawn independently at each time step.

- If $f(x,t) < \theta$ we employ a split-step numerical integration:
 - 1. Non-linear and diffusion terms. The term $\dot{f}(x,t) = D\nabla^2 f \sigma(t)f^2$ is integrated by means of the Runge-Kutta method obtaining a first solution f^* .
 - 2. Linear and stochastic terms. The term $\sigma(t)f + \sqrt{\frac{2}{N}f\xi(x,t)}$ is integrated in an exact way, see [3]:

$$f(x,t) = r_{\text{Gamma}} \{ r_{\text{Poisson}} \{ \lambda f^*(x,t) e^{\sigma(t)t} \} \} / \lambda.$$
(5)

being $\lambda = 2\sigma(t)/[\gamma^2 e^{\sigma(t)t}]$, and r_{Gamma} , r_{Poisson} random variables from Gamma and Poisson probability distributions respectively, i.e. $Prob[r_{\text{Gamma}}(a) = z] = z^{a-1}e^{-z}/\Gamma[a]$ and $Prob[r_{\text{Poisson}}(a) = z] = a^z e^{-a}/z!$.

To check the precision of our method we integrated the stochastic equation (3) for k = 0, $\alpha = 0$, and different growth rates s_s and compared the results to the analytical Fisher velocity $v_F = 2\sqrt{Ds_s}$. For large population size N, the velocity v of the wave asymptotically goes as $v_F - v \simeq C \ln^{-2}(N)$ [5]. Our numerical integration is consistent with this asymptotic relation from $N \simeq 10^4$ (figure 1A) with a root-mean-square deviation of 0.002. We have also obtained the values $(v_F - v)/v_F$ for the different growth rates employed in this work to obtain an estimation of the maximum error (see figure 1B). Note that v_F is not the actual velocity of the finite system, so the relative error $(v_F - v)/v_F$ is, in fact, smaller. The maximum error is around 0.9%, that, considering the results of figure 1A) leads to an overestimated error of about 0.0018%.

- Richard Courant, Kurt Friedrichs, and Hans Lewy, "On the partial difference equations of mathematical physics," IBM journal of Research and Development 11, 215–234 (1967).
- [2] Kirill S Korolev, Mikkel Avlund, Oskar Hallatschek, and David R Nelson, "Genetic demixing and evolution in linear stepping stone models," Reviews of modern physics 82, 1691 (2010).
- [3] Ivan Dornic, Hugues Chaté, and Miguel A Munoz, "Integration of langevin equations with multiplicative noise and the viability of field theories for absorbing phase transitions," Physical review letters **94**, 100601 (2005).
- [4] Haim Weissmann, Nadav M Shnerb, and David A Kessler, "Simulation of spatial systems with demographic noise," Physical Review E 98, 022131 (2018).
- [5] Éric Brunet and Bernard Derrida, "Effect of microscopic noise on front propagation," Journal of Statistical Physics 103, 269–282 (2001).