Fixation-Coexistence Transition in Spatial Populations

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Abstract – Balancing selection is a special case of frequency-dependent selection that is known to be the major force for the maintenance of biodiversity and polymorphism in natural populations. In finite populations, genetic drift eventually drives the population to fixation to the detriment of biodiversity. The interplay between selection and genetic drift is much richer in spatially-extended populations, where the local density of individuals can be low even in the limit of infinitely large systems. We consider the limit of very low local density of individuals (strong genetic drift) that is well represented by a modified voter model. We show analytically the existence of a non-equilibrium phase transition between a region in which fixation always occurs and a coexistence phase for a one-dimensional system. We also provide a characterization of the dynamical properties of the system, in particular for what concern the coarsening behavior and the existence of traveling waves.

Introduction. – The evolution of species should be firmly governed by the deterministic rules of Darwinian selection, but it is known since the seminal works by Wright and Fisher that the fate of biological populations can be strongly determined by chance [1]. This happens whenever selective forces are weak or absent (neutral theories) or in small populations, where random fluctuations induced by the discrete nature of individuals (*intrinsic noise*) cannot be neglected. Stochastic effects are relevant also in spatially-extended systems, in particular if there are regions characterized by a low density of individuals. This is a common situation at the population's front during range expansion [2] or in the case of spatial bottlenecks [3]. Experiments performed with microbial and yeast mutants on Petri dishes [4] are providing an extraordinary way to directly test the theoretical predictions, revamping the interest for low dimensional systems in theoretical population biology.

Over the years, analytical and numerical works have shed light on the interplay between intrinsic noise and spatial diffusion in neutral populations as well as in models with directional and frequency-dependent selection [5].

An interesting result, based on numerical simulations performed using either Kimura's stepping stone models [6] or appropriately modified voter models [7], relate to the existence of a fixation-coexistence phase transition in one-dimensional systems with negative frequency-dependent selection (or *balancing selection*).

Balancing selection is a major force for the maintenance of biodiversity, genetic heterozygosity and polymorphism in biological populations [8]. In a regime of strong competition, individuals carrying a rare genotype are able to exploit new resources, survive predation or better adapt to an evolving environment, gaining a fitness advantage. This advantage is transient, because it declines when the genotype becomes more common. This features have been recently observed experimentally in natural populations both at the phenotypic and genetic levels [9].

In this Letter, we study the strong noise limit of the one-dimensional dynamics with balancing selection, exploiting a formulation in terms of modified voter model that allows an analytical treatment. Using standard approximation methods, we provide a major understanding of the nature of the fixation-coexistence transition, explaining also the

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different dynamical properties observed in the two phases.

Voter Model with Balancing Selection. – In population genetics and in spatial ecology, interacting particle systems are used to describe diallelic populations or two-species competitive systems in the limit of very low density of individuals [10–12], in which the usual diffusion (Fokker-Planck) approximation of stepping-stone and island models is not fully mathematically justified. In this limit, the voter model is the prototype of neutral dynamics. In order to study balancing selection in one-dimensional populations, we adopt a modified dynamics inspired to the Neuhauser-Pacala (NP) model of spatial ecology [13]. We adapt the NP model to population genetics, following the work by Sturm and Swart [7]. The model is defined on a linear habitat of size L and periodic boundary conditions, in which each site i is occupied by one individual that can be of two possible "types" (e.g. two different alleles), that we represent by means of a spin-like formalism $S_i \in \{+1, -1\}$. At each microscopic time step, a site i is selected at random. With rate λ_0 the site i takes the value of a randomly selected neighbor (voter-like process), mimicking a neutral reproduction event. With rate $\lambda_b/2$, the spin flips if $S_{i+1} \neq S_{i+2}$ and again with rate $\lambda_b/2$ the spin-flip occurs if $S_{i-1} \neq S_{i-2}$. By means of the latter transitions an individual is replaced by a representative of the less frequent type in a contiguous triplet of sites, mimicking negative frequency dependent selection [7]. Since the rates of the transitions in opposite directions are equal, the rule generates an effective balancing selection force.

The one-dimensional dynamics can be mapped on that of branching-annihilation random walks with even off-springs (BARWe) [7]. Using field-theory, Cardy and Täuber [14] and more recently Canet et al. [15] noted that the critical behavior of the one-dimensional BARWe is not accessible using perturbative expansions from higher dimensions, because for $d < d'_c \approx 4/3$ it is controlled by a non-Gaussian fixed point of the RG flow. The latter should correspond to a continuous phase transition at some positive branching rate. The phase transition as function of λ_b and λ_0 was also found numerically by Sturm and Swart [7].

The Kirkwood Approximation. – A master equation for the evolution of the probability distribution $P(\vec{S}, t)$ of having the system in state $\vec{S} = \{S_1, \ldots, S_N\}$ at time t can be formally written from the spin-flip rates defined above. Computing the statistical averages, we get a hierarchy of equations for the multi-spin correlation functions [16] that cannot be solved exactly in any finite dimensional system. In one dimension, some progress can be obtained using a physically motivated moment closure approximation method, commonly known as the Kirkwood approximation [17].

The evolution equations for the local magnetization

$\langle S_i \rangle = \sum_{\vec{S}} S_i P(\vec{S}, t)$ and the pair correlation $\langle S_i S_j \rangle$ are

$$\frac{d\langle S_i \rangle}{dt} = \frac{\lambda_0}{2} [\langle S_{i-1} \rangle + \langle S_{i+1} \rangle - 2\langle S_i \rangle] \tag{1}$$
$$+ \frac{\lambda_b}{2} [\langle S_i S_{i-1} S_{i-2} \rangle + \langle S_i S_{i+1} S_{i+2} \rangle - 2\langle S_i \rangle]$$

$$\frac{d\langle S_i S_j \rangle}{dt} = \frac{\lambda_0}{2} [\langle S_i(S_{j+1} + S_{j-1}) \rangle \tag{2}$$
$$+ \langle S_j(S_{i+1} + S_{i-1}) \rangle - 4\langle S_i S_j \rangle]$$
$$+ \frac{\lambda_b}{2} [\langle S_i S_j(S_{i-1} S_{i-2} + S_{i+1} S_{i+2}) \rangle$$
$$+ \langle S_i S_j(S_{j-1} S_{j-2} + S_{j+1} S_{j+2}) \rangle - 4\langle S_i S_j \rangle].$$

Note that when j is close to i, some of the terms in the equation simplify. For instance if $j = i + 1$

$$\frac{d\langle S_i S_{i+1} \rangle}{dt} = \frac{\lambda_0}{2} [\langle S_i S_{i+2} \rangle + 2 + \langle S_{i-1} S_{i+1} \rangle \tag{3}$$
$$- 4\langle S_i S_{i+1} \rangle]$$
$$+ \frac{\lambda_b}{2} [\langle S_{i-2} S_{i-1} S_i S_{i+1} \rangle + \langle S_i S_{i+2} \rangle$$
$$+ \langle S_{i-1} S_{i+1} \rangle + \langle S_i S_{i+1} S_{i+2} S_{i+3} \rangle$$
$$- 4\langle S_i S_{i+1} \rangle].$$

The terms involving higher order averages can be factorized using the Kirkwood approximation [17],

$$\langle S_i S_{i+1} S_{i+2} \rangle \approx \langle S_i \rangle \langle S_{i+1} S_{i+2} \rangle \tag{4a}$$
$$\langle S_i S_{i-1} S_{i-2} \rangle \approx \langle S_i \rangle \langle S_{i-1} S_{i-2} \rangle \tag{4b}$$
$$\langle S_i S_j S_{i\pm1} S_{i\pm2} \rangle \approx \langle S_i S_j \rangle \langle S_{i\pm1} S_{i\pm2} \rangle \tag{4c}$$
$$\langle S_i S_j S_{j\pm1} S_{j\pm2} \rangle \approx \langle S_i S_j \rangle \langle S_{j\pm1} S_{j\pm2} \rangle. \tag{4d}$$

The choice of the above approximation scheme seems not to be mathematically justified, nevertheless it is the one that most accurately reproduces the mechanism of the non-linear microscopic process, in which a chosen spin flips only if an interface is present in the (left or right) nearest neighborhood. For random initial conditions (completely mixed population with equal fraction of the two genotypes), we can assume spatial translational invariance and introduce the time-dependent two-point correlation function $c_k(t) = \langle S_i S_{i+1+k} \rangle$. In this approximation, the temporal evolution of c_k is governed by the non-linear differential-difference equation

$$\dot{c}_0(t) = \lambda_0(c_1 + 1 - 2c_0) + \lambda_b(c_0^2 + c_1 - 2c_0) \tag{5a}$$
$$\dot{c}_1(t) = \lambda_0(c_2 + c_0 - 2c_1) + \lambda_b(c_1 c_0 + c_0 - 2c_1) \tag{5b}$$
$$\dot{c}_k(t) = \lambda_0(c_{k+1} + c_{k-1} - 2c_k) + 2\lambda_b(c_0 - 1)c_k, \tag{5c}$$

with $k > 1$ in the last line and $c_{-1}(t) = 1, \forall t$. In the following we show that (5) can be used to obtain approximate results on both the stationary and the long-time dynamics of the model.

Non-equilibrium Phase Transition. – Because of the non-linearity and non-locality of the differential-difference equations in (5), studying the dynamical processes that leads to the stationary states from random initial conditions requires some level of approximation. Let

us focus on the initial steps of the dynamics. Inserting $c_k(0) = \delta_{k,-1}$ in Eqs.(5) we find $\dot{c}_0(0) = \lambda_0 > 0$ and $\dot{c}_k(0) = 0$ for $k > 0$, therefore c_0 initially grows from zero while $c_k(t)$ stays zero until distance k is reached by diffusive transport from the boundary. We can thus safely assume that the short-distance correlation function relaxes to the stationary value $c_0^\infty = c_0(t = \infty)$ much faster than those at large distance. In this way, we can solve the dynamics of $c_k(t)$ for $k \gg 0$ under a quasi-stationary approximation, i.e. assuming that $c_0(t)$ takes its stationary value c_0^∞ in the rhs of Eq.(5c) and the initial conditions are modified to $c_k(0) = c_0^\infty \delta_{k,0}$. To find the stationary state for the nearest neighbors correlation function, we further assume that the domain walls between clusters of different types become sufficiently well separated at long times, so that we can solve Eq.5a with $c_1^\infty \simeq c_0^\infty$. The assumption is certainly valid in the continuous space limit, because the typical cluster size at long times will be much larger than the microscopic lattice spacing. Thus for convenience we take the continuum limit, defining $c(r,t) = c_{ka}(t)$ with $r = ka$ and sending the lattice spacing a to zero. In the simulations a is finite, but the continuum limit emerges for the effective macroscopic dynamics when we take sufficiently large system size L, as it corresponds to scale down the lattice spacing as $a \propto 1/L$ with the total system size kept fixed to 1. Eq.5a admits two stationary states: $c_0^\infty = 1$ for $\lambda_b < \lambda_0$ and $c_0^\infty = \lambda_0/\lambda_b$ for $\lambda_b \geq \lambda_0$. Let us verify whether this change in the local behavior corresponds to a non-equilibrium phase transition for an infinite system.

For $\lambda_b < \lambda_0$, the evolution equation of $c(r,t)$, obtained inserting the stationary value $c_0^\infty = 1$ in Eq.5c and taking the continuum limit is

$$\dot{c}(r,t) = D\partial_r^2 c(r,t) \qquad (6)$$

with boundary condition $c(r,0) = \delta(r)$ and diffusion constant $D \propto \lambda_0$. Eq.6 says that, at sufficiently large times, the transitions with rate λ_b have no effect on the dynamics, which is dominated by diffusion and annihilation of domain walls exactly like in the voter model [16]. The stationary solution is trivially $c(r,\infty) = 1 \; \forall r$, i.e. the system eventually reaches fixation into the absorbing state. The result can be conveniently expressed in terms of the average spatial heterozygosity $H(r,t) = (1 - c(r,t))/2$, that represents the probability that at time t two individuals at distance r are different [5]. For random initial conditions, with equal fraction of the two types, the average local heterozygosity decays as $H(0,t) = (1-c(0,t))/2 \propto (4\lambda_0 t)^{-1/2}$ for $t \to \infty$.

When instead $\lambda_b > \lambda_0$, the evolution equation at distances $r \gg 0$ becomes

$$\dot{c}(r,t) = D\partial_r^2 c(r,t) - 2(\lambda_b - \lambda_0)c(r,t), \qquad (7)$$

with $c(0,t) = \lambda_0/\lambda_b$, $c(r,0) = \lambda_0/\lambda_b \delta(r,0)$, and D is a diffusion constant that emerges from the spatial rescaling. Solving the equation we find $c(r,\infty) = (\lambda_0/\lambda_b)e^{-|r|/\xi}$
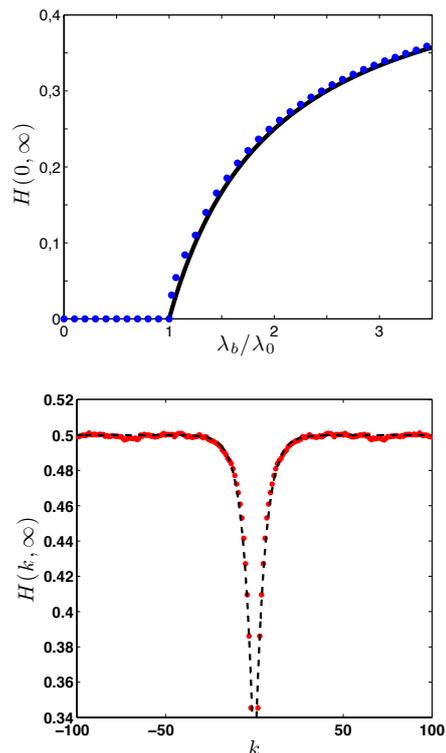

Fig. 1: Top: Average local heterozygosity $H(0,\infty)$ in the stationary state as a function of λ_b/λ_0: numerical simulations (blue points) performed on a system of size $L = 10^3$ are compared with the approximated analytical prediction obtained solving Eq. (5a) with the assumption $c_1^\infty \simeq c_0^\infty$ (black full line). Bottom: Average heterozygosity $H(k,\infty)$ in the stationary state as function of the distance k for $\lambda_b/\lambda_0 = 2.5$. The results of numerical simulations (red dots) are complemented by a fit from the theory (dashed line).

with $\xi^2 \propto 1/(\lambda_b - \lambda_0)$, a result that is qualitatively correct up to an arbitrary rescaling of the spatial length-scale (that corresponds to fix the value of the diffusion constant D). The time-dependent behavior is then obtained by adding a solution of the homogeneous differential equation in which $c(0,t)$ vanishes at all times. It is easy to see that all time-dependent terms decay to the stationary state $c(r,\infty)$ exponentially fast, with rate $\propto \lambda_b - \lambda_0$.

In summary, the stationary behavior of the average local heterozygosity $H(0,\infty)$ predicts a phase transition at $\lambda_b = \lambda_0$ from a region in which the system fixates into one of the two symmetric homogeneous absorbing states (i.e. $H(0,\infty) = 0$) to an active phase of non-trivial coexistence in which $H(0,\infty) = (1 - \lambda_0/\lambda_b)/2$. We have verified these theoretical predictions performing numerical simulations of the microscopic spin-flip model. In a finite system, the population eventually fixates to one of the two absorbing states for all values of λ_b/λ_0. However, in the absorbing phase the time necessary to reach fixation scales as L^2, whereas above the critical point coexistence

survives for times that scale exponentially with the system size L. Hence, the phase transition in the stationary state can be safely studied numerically on a finite, but sufficiently large, system (e.g. $L = 10^{3 \div 4}$). In the top panel of Figure 1, we display the behavior of the "order parameter" $H(0, \infty)$ vs. λ_b/λ_0 obtained from numerical simulations (blue points) that turns out to match perfectly the curve computed in the Kirkwood approximation (full line). The bottom panel of Fig.1 shows the stationary profile of the spatial heterozygosity in the coexistence phase (red points). The shape of the profile converges exponentially fast to $1/2$ with the distance k from the origin and it is in good qualitative agreement with the theoretical predictions (dashed line). The theoretical curve is obtained by fitting the numerical results using the functional form provided by the solution of Eq.(7), with the diffusion coefficient D as fitting parameter.

The coarsening regime for the long-time dynamics of the microscopic spin-flip model for $\lambda_b < \lambda_0$ is shown in Fig.2. Clusters growth is evident from the time-oriented snapshots in top panel. In the bottom panel we show the time evolution of $H(0, t)$, that is characterized by a power law decay with exponent ≈ -0.5. Since the average domain length can be roughly estimated as $\ell(t) \propto 1/H(0, t)$, we can then conclude that the system is characterized by a scaling regime where domains grow as $\ell(t) \sim t^n$ with coarsening exponent $n = 1/2$.

Fixation Probability. – Another interesting quantity that characterizes the absorbing state is the fixation probability of one of the two types as a function of the initial proportion of the types. Because of the Z_2 symmetry, this corresponds to compute the probability $P_\uparrow(F_0)$ that a system with initial average density F_0 of "up" individuals ends up into the absorbing state with all individuals being "up". Within the Kirkwood approximation, we can solve the evolution equation for the average density of type "up", $F(t) = (1 + \langle S_i \rangle)/2$ and compute $F(\infty)$ that is the mean-field expression for $P_\uparrow(F_0)$. Applying the decoupling scheme to Eq.1, we integrate the local dynamics assuming that the value of $F(t)$ is still close to the initial one when the approximation $c_1(t) \simeq c_0(t) = 1 - 2H(0, t)$ starts to hold. The corresponding equations are

$$\frac{\partial F}{\partial t} = -\lambda_b(2F - 1)H(0, t), \tag{8a}$$

$$\frac{\partial H(0, t)}{\partial t} = (\lambda_b - \lambda_0)H(0, t) - 2\lambda_b H(0, t)^2 \tag{8b}$$

with initial conditions $F(0) = F_0$ and $H(0, 0) = 2F_0(1 - F_0)$. Solving the equations, we get $H(0, t) = (\lambda_b - \lambda_0)/\left[2\lambda_b + Ce^{-(\lambda_b - \lambda_0)t}\right]$ with $C = (\lambda_b - \lambda_0)/(2F_0(1 - F_0)) - 2\lambda_b$ and $F(t) = \frac{1}{2}\left\{1 + \frac{(\lambda_b - \lambda_0)(2F_0 - 1)}{\lambda_b - \lambda_0 + 4\lambda_b F_0(1 - F_0)(e^{(\lambda_b - \lambda_0)t} - 1)}\right\}$. The stationary solution in the limit $t \to \infty$ gives

$$F(\infty) = \begin{cases} \frac{1}{2}\left[1 + \frac{(\lambda_0 - \lambda_b)(2F_0 - 1)}{\lambda_0 + \lambda_b(4F_0(1 - F_0) - 1)}\right] & \text{if } \lambda_b < \lambda_0, \\ \frac{1}{2} & \text{otherwise}. \end{cases} \tag{9}$$
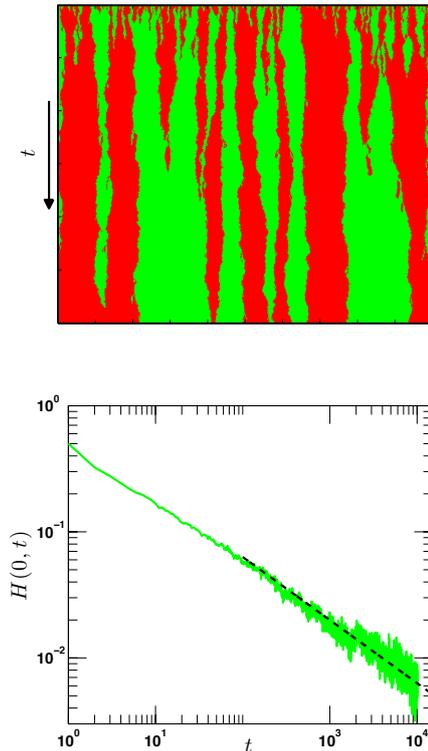

Fig. 2: Top: 1+1 dimensional snapshot of the evolution of a system of size $L = 10^4$ starting from random initial conditions into the absorbing phase ($\lambda_b = 0.5$). Bottom: temporal decay of the average local heterozygosity $H(0, t)$ for $\lambda_b = 0.5$, the dashed line indicates a power-law decay $\propto t^{-0.5}$.

Obviously in the coexistence region, fixation events are finite-size effects with the two absorbing states being equally probable. In the absorbing region instead, we can suppose that the local dynamics converges to a quasi-stationary state, with values $F(\infty)$ and $H(0, \infty)$, that acts as a sort of initial condition for the voter-like coarsening process leading to fixation. During the latter, the fixation probability is not expected to change, because it is known that the fixation (or exit) probability of a voter-like process is linear in its initial conditions. Figure 3 displays the fixation probability $P_\uparrow = F(\infty)$ as function of the initial density F_0 computed through Eq.9 for different values of $\lambda_b < \lambda_0$ along with a comparison with numerical simulations. The overall agreement is good. We observe in particular that the probability flattens along the $F(\infty) = 1/2$ line as λ_b gets closer to λ_0, according to the fact that for $\lambda_b > \lambda_0$ a stationary state with non-zero heterozygosity is always reached in infinitely large systems. It is remarkable that even though the long-time dynamics in the absorbing phase is completely similar to that observed for the pure voter model, the exit probability is not linear with F_0, and explicitly depends on the value of λ_b.
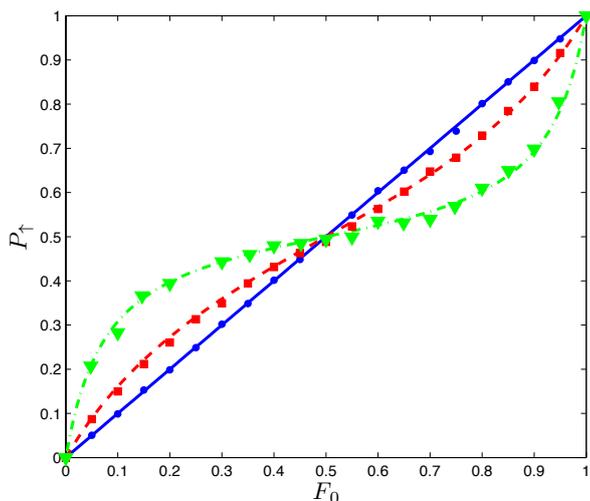
Fig. 3: Fixation probability $P_\uparrow$ of one type when the initial conditions are random with a density F_0 of individuals of that type. Points refer to numerical simulations, while lines to the analytic result reported in the main text. Blue dots and blue solid lines: $\lambda_b = 0.0$. Red squares and red dashed line: $\lambda_b = 1/3$. Green triangles and green dot-dashed line: $\lambda_b = 3/4$. In all cases $\lambda_0 = 1.0$. The theoretical predictions in Eq. (9), obtained using the Kirkwood approximation, are in good agreement with the results of numerical simulations. Consistently with the fact that for $\lambda_b > \lambda_0$ the stationary state displays coexistence of the two populations, we observe that the exit probability tends to flatten along the $P_\uparrow = 1/2$ line as λ_b gets closer to $\lambda_0 = 1$.

Balancing Waves. – Spatial populations are often subject to invasions and expansion events. In the present case, we are interested in understanding in which way balancing selection could favor the propagation of polymorphism in a completely homogenous environment. We consider the invasion of a new type into a homogeneous phase. When the conditions for coexistence are satisfied (i.e. $\lambda_b > \lambda_0$), the stable polymorphic phase propagates into the unstable monomorphic one by means of Fisher-like traveling waves [19], that we call "balancing waves". To demonstrate this mechanism, we consider a system prepared in a completely ordered state (e.g. all individuals belonging to one type) with a small localized defect in which both types can be present. An equation of motion for the front between the two phases can be derived from (3) relaxing the assumption of spatial homogeneity. Using the Kirkwood approximation without assuming translational invariance, we obtain the equation

$$\frac{d\langle S_i S_{i+1}\rangle}{dt} = \frac{\lambda_b}{2}\langle S_i S_{i+1}\rangle\left[\langle S_{i-2}S_{i-1}\rangle + \langle S_{i+2}S_{i+3}\rangle - 2\right]$$
$$+ \frac{\lambda_0 + \lambda_b}{2}\left[\langle S_i S_{i+2}\rangle + \langle S_{i-1}S_{i+1}\rangle\right.$$
$$\left. -2\langle S_i S_{i+1}\rangle\right] + \lambda_0\left[1 - \langle S_i S_{i+1}\rangle\right]. \quad (10)$$

To describe the front we use the average local heterozygosity at site i, $\bar{h}_i = (1 - \langle S_i S_{i+1}\rangle)/2$ which vanishes in

the homogeneous phase while it is finite in the coexistence one. Because of the lack of translational invariance, the difference $\langle S_{i-1}S_{i+1}\rangle - \langle S_i S_{i+1}\rangle$ now quantifies the local variation of the heterozygosity at the front. A diffusive contribution emerges in the continuum limit,

$$\langle S_{i-1}S_{i+1}\rangle + \langle S_i S_{i+2}\rangle - 2\langle S_i S_{i+1}\rangle$$
$$= -\Delta\bar{h}_i(t) + \langle(S_{i-1} - S_{i+2})(S_{i+1} - S_i)\rangle \approx -\Delta\bar{h}_i(t)$$
$$\propto -\partial_x^2 \bar{h}(x,t).$$

Notice that the term $\langle(S_{i-1} - S_{i+2})(S_{i+1} - S_i)\rangle \approx 0$ at the front between the two phases because, on average, $S_{i-1} \neq S_i$ while $S_{i+1} = S_{i+2}$. In addition, the heterozygosity selection process gives the contribution

$$\langle S_i S_{i+1}\rangle(\langle S_{i-2}S_{i-1}\rangle + \langle S_{i+2}S_{i+3}\rangle - 2)$$
$$= (1 - 2\bar{h}_i)\left[1 - 2\bar{h}_{i-2} + 1 - 2\bar{h}_{i+2} - 2\right]$$
$$= -2(1 - 2\bar{h}_i)\left[\bar{h}_{i-2} + \bar{h}_{i+2}\right]$$
$$\approx -4\left[1 - 2\bar{h}(x,t)\right]\bar{h}(x,t)$$

where we neglected higher-order diffusive terms. Putting all terms together we obtain the well-known Fisher-Kolmogorov-Petrovskii-Piscounov (FKPP) equation [19, 20]

$$\frac{\partial\bar{h}}{\partial t} = D\frac{\partial^2\bar{h}}{\partial x^2} + (\lambda_b - \lambda_0)\bar{h} - 2\lambda_b\bar{h}^2, \quad (11)$$

where $D \propto \lambda_b + \lambda_0$. Suppose that we prepare the system in the homogeneous state everywhere (e.g. all individuals of "up" type), except for a spatially localized region in which $\bar{h}(x,0) > 0$. For $\lambda_b > \lambda_0$, in this region the heterozygosity will approach rapidly the stable non-zero stationary value and by diffusion the coexistence phase will expand in the homogeneous region. The propagation occurs by means of a traveling wave of the form $\bar{h}(x,t) \sim e^{-\alpha(x-vt)}$ where α is a constant related to the initial profile of the front and the velocity can be computed from the linearized expression of (11), $v = 2\sqrt{D(\lambda_b - \lambda_0)}$ [16]. Because of the existence of traveling waves, the expansion of the stable coexistence phase occurs in a ballistic way. The validity of this analysis is proved numerically in Fig.4. As expected the size of the coexistence region increases linearly with time (bottom left panel), at a velocity that grows with the distance from the critical point, i.e. with $\lambda_b - \lambda_0$.

Conclusions. – In this Letter, we investigated the interplay between the Moran process of random reproduction and the balancing selection in the presence of spatial structure. Using a spin-like representation, very common in theoretical biology, we explored the limiting behavior of a population when it is characterized by a very small local density of individuals. We obtained an accurate picture of the behavior of the population in the different dynamical regimes that matches very well the results of numerical simulations and provides a clear explanation of the underlying mechanisms. Our results in one-dimensional systems

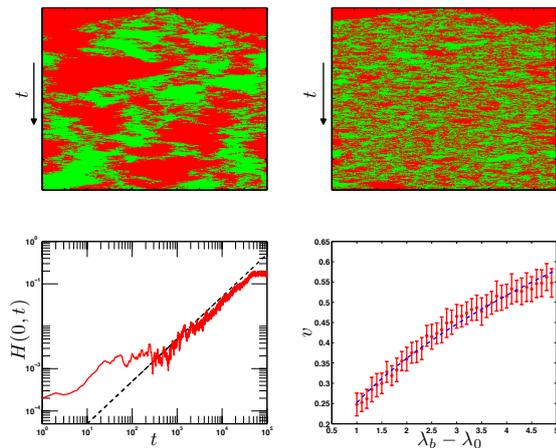Luca Dall'Asta1,2, Fabio Caccioli3 Deborah Beghè4

Fig. 4: Top: 1+1 dimensional snapshots of the evolution of a system of size $L = 10^4$ starting from a single defect towards the stationary active phase for $\lambda_b = 1.05$ (left) and 1.5 (right). Bottom left: time evolution of $H(0,t)$ for a system of size 10^4 with $\lambda_b = 2.5$, $\lambda_0 = 1$ and initial condition corresponding to a single defect. The dashed line is a linear fit. A linear growth of the average local heterozygosity corresponds to a ballistic expansion of the coexistence phase. Bottom right: propagation velocity of balancing waves as a function of $\lambda_b - \lambda_0$. Points refer to numerical simulations, while the dashed blue line is a square root function. Starting from a single defect, the size of the coexistence zone increases linearly with time with a velocity that depends on $\lambda_b - \lambda_0$.

can be viewed as the first step in order to understand the role of balancing (and in general frequency-dependent) selection in more complex setups, such as the front of a population during range expansion. The fixation-coexistence phase transition found in our model has been observed numerically in a recent work by Korolev and Nelson [6] using a stepping-stone model with a larger local density of individuals. Hence, one could consider our results as the limiting behavior of the stepping-stone model in a regime of strong genetic drift. A direct connection between the two models will be presented elsewhere.

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