Nonmonotonic Effects of Migration in Subdivided Populations

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The influence of migration on the stochastic dynamics of subdivided populations is still an open issue in various evolutionary models. Here, we develop a self-consistent mean-field-like method in order to determine the effects of migration on relevant nonequilibrium properties, such as the mean fixation time. If evolution strongly favors coexistence of species (e.g., balancing selection), the mean fixation time develops an unexpected minimum as a function of the migration rate. Our analysis hinges only on the presence of a separation of time scales between local and global dynamics, and therefore, it carries over to other nonequilibrium processes in physics, biology, ecology, and social sciences.

Natural populations are often subdivided and fragmented in space, with the consequence that species or genetic traits become locally extinct and recolonized by migration. Understanding and predicting how migration among subpopulations affects their collective evolution is, therefore, an important issue across various disciplines, e.g., conservation ecology [1], population genetics [2], evolutionary game theory [3], language competition [4], learning dynamics [5], and epidemics [6].

The dynamics of subpopulations results from the competition between the evolutionary "force" (selection) which favors stronger genotypes and the intrinsic noise (genetic drift) due to death and reproduction of individuals. This noise eventually drives any finite population into an absorbing state (fixation), in which all individuals have the same traits (e.g., species, language, opinion). In subdivided populations, migration acts with selection and internal noise, influencing the statistical properties of the fixation process, such as the mean fixation time (MFT). In this respect, it is widely accepted that in the absence of spatial embedding, the effect of subdivision in populations of constant and equal size effectively amounts at a rescaling of the relevant parameters of the population, such as the population size and the effective strength of the selection [7,8]. When selection is constant or absent, the MFT monotonically decreases upon increasing the migration rate [4,9,10], but more complex behaviors cannot be ruled out *a priori*. Here, we consider evolutionary forces that favor biodiversity, i.e., the coexistence of species or different genotypes, showing that the MFT can, in fact, display a nonmonotonic dependence on the migration rate. Even in the absence of mutation, this kind of evolutionary forces are common in the evolution of natural populations. For instance, the so-called balancing selection [2,11] acts in several contexts, most notably mammalian [12] and plants [13]. The maintenance of some genetic diseases in humans, e.g., sickle-cell anemia [14], thalassemia [15], and cystic fibrosis [16], is

also ascribed to balancing selection. Analogous mechanisms are responsible for cooperative behaviors in ecology and coevolutionary dynamics [17,18], such as those recently observed in microbial communities [19], or for emergent bilingualism in language competition [20].

For concreteness, we focus, here, on a model specific to population genetics, and we investigate the effect on the MFT of the interplay between balancing selection and subdivision. We develop a self-consistent mean-field-like approach which yields an effective dynamic equation, from which we derive the nonequilibrium collective properties, such as the MFT. For weak selection, our approximation renders the one of Ref. [10]. We show that the MFT can actually develop a minimum as a function of the migration rate for sufficiently strong selection. This is in contrast to the assumptions in Ref. [8] and to the intuitive idea that the collective fluctuation needed to reach global fixation could be facilitated by increasing the migration. The existence of this minimum depends, *inter alia*, on the optimal frequency, i.e., on the amount of biodiversity promoted by balancing selection alone. The nonmonotonicity of the MFT is reflected in the behavior of the so-called "heterozygosity," which quantifies the biodiversity within the subdivided population.

The model.—Inspired by common models in population genetics, we consider $\Omega \gg 1$ individuals carrying a single copy of a gene with two possible values (alleles) A and B. The evolution of this large but finite population turns out to be effectively described by a diffusion approximation [21,22], i.e., by a Langevin equation for the frequency x of, e.g., allele A. The mean change of x in a well-mixed population is $\mu(x) = \tilde{s}x(1-x)$, where $\tilde{s}$ is the selection rate, while the variance is approximately given by $v(x) = x(1-x)/(\Omega\tau_g)$, where τ_g is the generation time (see Ref. [23] for a derivation of these expressions from microscopic models). Hereafter, time is measured in units of generations, so that $\tau_g = 1$ and the rates become

dimensionless quantities. Balancing selection is characterized by $\tilde{s} = s(x_* - x)$, where $s > 0$ is a constant and x_* represents the internal optimal frequency which is promoted by balancing effects in an infinite population.

In order to investigate the influence of migration on subdivided populations with balancing selection in the simplest possible setting, we consider the celebrated Island model, originally proposed by Wright [29] for neutral evolution. It consists of N subpopulations (demes), each composed of Ω individuals which evolve as described above [with the same $\mu(x)$ and $v(x)$], while being allowed to exchange a randomly picked individual with any other deme at a rate m/N, such that Ω is unchanged. For sufficiently large Ω and small m and s, the evolution of the allele frequency $x_i \in [0, 1]$ in the ith deme is described by the Langevin equation [21,23] (with Itô prescription)

$$\dot{x}_i = \mu(x_i) + m(\bar{x} - x_i) + \sqrt{v(x_i)}\eta_i, \quad (1)$$

where η_i are independent Gaussian noises with $\langle \eta_i(t)\eta_j(t')\rangle = \delta_{i,j}\delta(t - t')$; hereafter, the overbar denotes interdeme averages, e.g., $\overline{x^k} = \sum_i x_i^k/N$, and thus, $\bar{x}$ is the interdeme mean frequency (IDMF). For $m = 0$, the demes are independent: the deterministic selection term μ in Eq. (1) drives x_i towards x_*, while the random genetic drift finally drives x_i towards one of the two possible absorbing states $x_i = 0$ and 1, corresponding to fixation of allele B and A, respectively [see Fig. 1(a)]. For $m > 0$, migration acts as a source of biodiversity for the subpopulations, preventing their independent fixation [see Figs. 1(b) and 1(c)] and favoring a coordinate evolution of the interacting demes. For $\Omega m \gg 1$ and x_* sufficiently close to 0 or 1, the collective evolution rapidly drives all demes into the same absorbing state; instead, for a wide range of parameters, the IDMF $\bar{x}$ fluctuates for a long time around a value $\hat{x}$—characterized by the vanishing of the deterministic force in the dynamics of $\bar{x}$—until fixation eventually occurs through a rare (for large N) fluctuation ([23], Sec. S2B). This coordinated behavior around $\hat{x}$ becomes effectively a metastable state if the typical time T_{rel} required to reach it from the initial condition is significantly shorter than the typical time T_{fluct} for fixation to occur. This condition is satisfied for $ms\Omega^2 N \gg 1$ ([23], Sec. S2A). The statistics of fixation can be studied by considering the evolution equation of $\bar{x}$, which follows from Eq. (1):

$$\dot{\bar{x}} = s[x_*\bar{x} - (1 + x_*)\overline{x^2} + \overline{x^3}] + \sqrt{(\bar{x} - \overline{x^2})/(\Omega N)}\eta, \quad (2)$$

where η is a Gaussian noise with $\langle \eta(t)\eta(t')\rangle = \delta(t - t')$. This equation involves higher-order moments, and the hierarchy does not close; however, we can proceed by introducing a moment closure scheme based on a self-consistent mean-field-like approximation.

The approximation.—Since the global variable $\bar{x}$ is the average of N local frequencies, it is heuristically
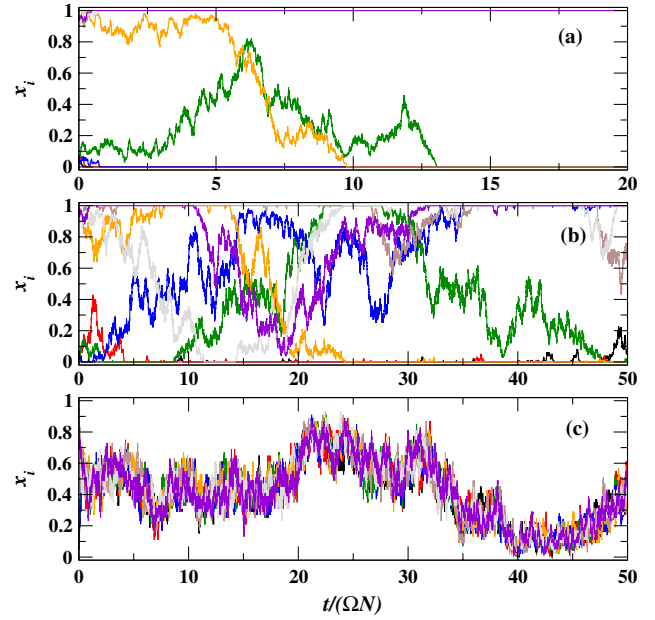

FIG. 1 (color online). Time evolution of the frequency x_i of allele A in the various demes (represented by different colors) of a fully connected population consisting of $N = 8$ demes with $\Omega = 100$ individuals each (a) in the absence of migration ($m = 0$) or (b) for small ($\Omega m = 0.05$) and (c) large ($\Omega m = 50$) migration rate. The balancing selection is characterized here by $x_* = 0.5$ and $\Omega s = 5$. At time $t = 0$, half of the demes have $x_i = 0.05$, while the remaining ones $x_i = 0.95$. Upon increasing N, the fluctuations of $\bar{x}$ around x_* reduce significantly in panel (c).

expected that its dynamics is much slower than that of the individual $\{x_i\}$, determining a separation of time scales between the local and global dynamics. In the absence of selection ($s = 0$), Eq. (2) is driven only by the genetic drift; therefore, the time scale separation occurs for sufficiently large N ($N\Omega m \gg 1$). Being coupled only via the slowly varying quantity $\bar{x}$, $\{x_i\}$ can be considered as almost independent random variables, each one described by a conditional quasistationary distribution $P_{\text{qs}}(x_i|\bar{x})$. The latter can be obtained by solving the stationary Fokker-Planck equation associated with Eq. (1), in which $\bar{x}$ is treated as a constant parameter. Under these assumptions the population average $\overline{x^k}(t)$ can be approximated, for $N \gg 1$, by the corresponding mean $\int dx_i\, x_i^k P_{\text{qs}}(x_i|\bar{x})$. For $s = 0$, one obtains $P_{\text{qs}}(x|\bar{x}) \propto x^{2m'\bar{x}-1}(1-x)^{2m'(1-\bar{x})-1}$, where $m' = \Omega m$ is a rescaled rate introduced for convenience and $P_{\text{qs}}(x|\bar{x})$ satisfies the consistency condition $\bar{x} = \int_0^1 dx\, x P_{\text{qs}}(x|\bar{x})$. This $P_{\text{qs}}(x|\bar{x})$ can then be used for evaluating $\overline{x^2}$ and $\overline{x^3}$ in Eq. (2) and for calculating the mean drift $M(\bar{x})$ and variance $V(\bar{x})$ of the (stochastic) variable $\bar{x}$ [10]

$$M(\bar{x}) = s_e\bar{x}(1 - \bar{x})(x_*^e - \bar{x}) \quad \text{and} \quad V(\bar{x}) = \frac{\bar{x}(1 - \bar{x})}{N_e}. \quad (3)$$
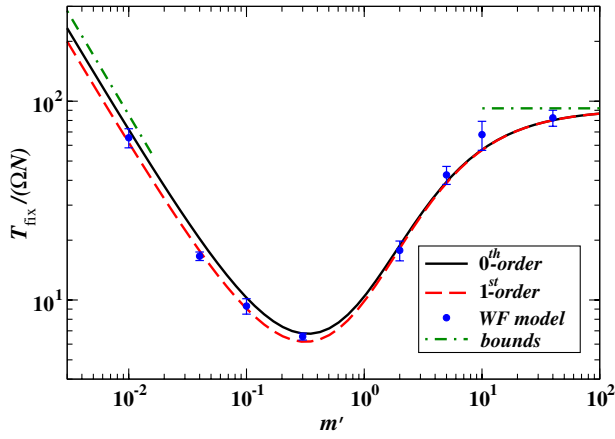
FIG. 2 (color online). Mean fixation time as a function of the migration rate m' with $N = 30$, $\Omega = 100$, $s' = 1$, and $x_* = 0.5$. The solid line corresponds to Eq. (5), while the dashed line accounts for the first-order correction in s_e/m; symbols with error bars are the results of numerical simulations of the WF model. The dashed-dotted lines indicate the upper bounds for small and large migration, found in Ref. [8].

This implies that at the lowest nonvanishing order in s, the subdivided population behaves like a well-mixed one with an effective selection coefficient $s_e = s/[(1 + (1/m'))(1 + (1/2m'))]$, an effective population size $N_e = N\Omega(1 + (1/2m'))$, and an effective optimal frequency $x_*^e = x_* + (x_* - 1/2)/m'$. The time scale T_{migr} associated with the response of x_i to a variation of $\bar{x}$ can be read from Eq. (1) and it is $T_{migr} \simeq 1/m$. The typical time scale of the dynamics of $\bar{x}$ is determined, instead, either by the time scale $T_{rel} \simeq 1/s_e$ of the drift or by the time scale $T_{fluct} \simeq N_e$ of the stochastic term in Eq. (3). When $T_{rel} < T_{fluct}$, i.e., $N\Omega s > 1 + 1/m'$, our approximation requires $T_{rel} \gg T_{migr}$, i.e., $s_e \ll m$, while in the opposite case, it is accurate whenever $N \gg 1$ (see Ref. [23], Sec. S2A for a detailed discussion). This approximation can be generalized to small but nonvanishing values of s_e/m by accounting (a) for $s \neq 0$ in the quasistationary distribution P_{qs}, and (b) for the fact that $\bar{x}$ slowly changes during the fast evolution of x_i, which results in a distribution $P_{qs}(x_i|y(t))$ where the effective field $y(t) \simeq \bar{x}(t)$ has to be determined self-consistently. The single-deme quasistationary distribution for $s' \equiv \Omega s \neq 0$ is

$$P_{qs}(x|y) \propto x^{2m'y-1}(1-x)^{2m'(1-y)-1}e^{s'x(2x_*-x)}. \quad (4)$$

The consistency condition $\bar{x} = \int_0^1 dx\, x P_{qs}(x|y)$ gives $y = \bar{x} - (s_e/m)\bar{x}(1-\bar{x})(x_*^e - \bar{x}) + O((s_e/m)^2)$, which can be used together with Eq. (4) in order to calculate higher-order corrections in s to $M(\bar{x})$ and $V(\bar{x})$ ([23], Sec. S3).

Mean fixation time.—On the basis of $M(\bar{x})$ and $V(\bar{x})$ calculated as discussed above, the MFT $T_{fix}(\bar{x})$ for the whole population with an initial IDMF $\bar{x}$ is determined

within the diffusion approximation by $V(\bar{x})T_{fix}''(\bar{x})/2 + M(\bar{x})T_{fix}'(\bar{x}) = -1$ [30]. For $x_* = 1/2$, by using the lowest-order approximations [$^{(0)}$] for M and V in Eq. (3) and choosing the state $\bar{x} = 1/2$ (corresponding to the metastable state) as the initial condition, we get

$$T_{fix}^{(0)} = N_e \int_0^1 dy \int_0^1 dz \frac{e^{s_e N_e y(1-z^2)/4}}{1 - yz^2}, \quad (5)$$

which reaches a constant value for $m' \gg 1$, while $T_{fix}^{(0)}/(N\Omega) \simeq \log 2/m'$ for $m' \ll 1$. Figure 2 shows $T_{fix}^{(0)}$ (solid line) as a function of m' for the population specified in the caption, together with the prediction (dashed line) which accounts for the first-order correction in s_e/m to the mean drift $M(\bar{x})$ and variance $V(\bar{x})$ [23]. $T_{fix}^{(0)}$ shows a marked nonmonotonic dependence on the migration rate m', while complying with the bounds of Ref. [8] for small and large m' (dashed-dotted lines). In fact, $T_{fix}^{(0)}(m' \gg 1)$ approaches the value it would have in a well-mixed population of ΩN individuals, whereas for $m' \ll 1$, fixation— and thus, T_{fix}—is controlled by the growing time scale $T_{migr} \propto 1/m'$ associated with migration. In this respect, the limit $m' \to 0$ differs essentially from the case $m' = 0$, in which T_{fix} is governed by the single-deme fixation times, is finite, and scales $\propto \log N$ for large N ([23], Sec. S4).

In order to demonstrate the accuracy of our analytical predictions, Fig. 2 reports the results (symbols with error bars) of numerical simulations of the Wright-Fisher (WF) microscopic model with balancing selection [23]. Their agreement with the analytical prediction of Eq. (5) is very good and further improves upon including the first-order corrections in s_e/m (dashed line).

Figure 3(a) shows that the nonmonotonicity displayed in Fig. 2 is enhanced upon increasing $\sigma \equiv s'N$, while it disappears for $\sigma < \sigma_c$, where $\sigma_c \simeq 5.2$ is a critical threshold below which the MFT behaves qualitatively as in a neutral population with $s = 0$. The value m'_{min} of m' at which T_{fix} is minimum diverges for $\sigma \to \sigma_c$ and decreases upon increasing $\sigma > \sigma_c$, as shown in Fig. 3(b). The value σ_c slightly depends on s_e/m if the corrections to Eq. (3) are included. Figure 3(c) shows that the nonmonotonicity of $T_{fix}^{(0)}$ also persists for $x_* \neq 1/2$, but only within an interval of values of x_* which depends on σ—as indicated by the shaded area in Fig. 3(d)—and which covers the entire range for $\sigma \gtrsim 10$.

Biodiversity.—Migration is expected to affect the level of biodiversity of a population. In diallelic models, this effect is usually studied in terms of (i) the global heterozygosity $H = 2\bar{x}(1 - \bar{x})$, which quantifies the diversification of the global population but neglects the possible subdivision in demes, and (ii) the intrademe heterozygosity $h = (2/N)\sum_{i=1}^N x_i(1 - x_i) = 2\overline{x(1-x)}$, which measures the average level of diversification inside each deme. Note that $0 \leq h \leq H \leq 1/2$. $H = 0$ corresponds to the loss of global biodiversity, namely all individuals within the population have the same genotype; $H = 1/2$, instead,
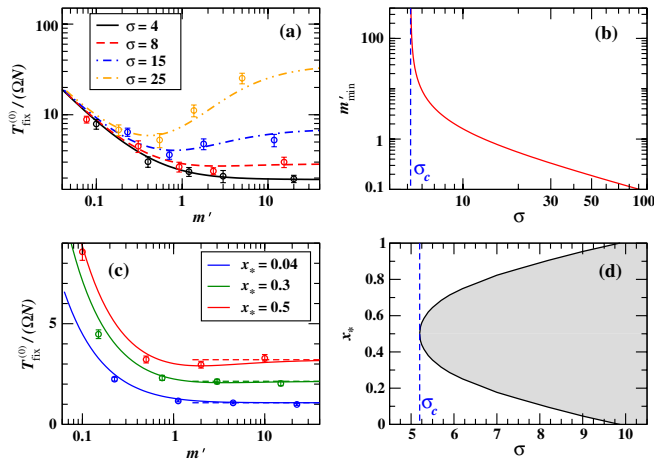
FIG. 3 (color online). Features of the mean fixation time $T_{\text{fix}}^{(0)}$ in Eq. (5) for a population of $N = 30$ demes with $\Omega = 100$ individuals each: (a) dependence of $T_{\text{fix}}^{(0)}$ on m' for $x_* = 0.5$ and various values of σ; (b) $m'_{\min}$ as a function of σ; (c) $T_{\text{fix}}^{(0)}$ as a function of m' for $\sigma = 9$ and various x_*; (d) region (gray) of the parameter space (σ, x_*) where $T_{\text{fix}}^{(0)}$ is a nonmonotonic function of m'. Symbols with error bars are the results of numerical simulations of the WF model.

corresponds to the maximal possible global biodiversity in which the two genotypes are equally present within the whole population. Analogous interpretation holds for $h = 0$ and $h = 1/2$ at the intrademe level. As depicted in Fig. 1(c), the local allele frequencies $\{x_i\}$ approach each other for $m' \gg 1$, with $x_i \simeq x_j$, and therefore, $h \simeq H$. In the case of the moderate migration rate $m' \lesssim 1$ of Fig. 1(b), instead, different demes fix different alleles, causing $h \simeq 0$, while H is maintained positive by migration which acts as a constant source of biodiversity.

In order to understand how migration affects biodiversity before the eventual fixation $H = h = 0$, we assume that the population at time $t = 0$ is in the metastable state $\bar{x} = \hat{x}$ such that $H(0) = 2\hat{x}(1 - \hat{x})$, and that it persists in this state until fixation occurs. Under this heuristic assumption, one can approximate $H(t) \simeq [1 - p_{\text{fix}}(\hat{x}, t)]H(0)$, where $p_{\text{fix}}(x_0, t)$ is the probability that a population prepared with $\bar{x} = x_0$ at time $t = 0$ has already fixed at time t. p_{fix} satisfies the backward Fokker-Planck equation $\partial_t p_{\text{fix}} = M(x_0)\partial_{x_0} p_{\text{fix}} + V(x_0)\partial_{x_0}^2 p_{\text{fix}}/2$, which can be integrated numerically. By using the expressions of M and V in Eq. (3), the results of this approximation for H are presented in Fig. 4 as functions of m' for some values of t, and they are compared with those of numerical simulations of the WF model (symbols with error bars) [23]. Note that the estimate of $H(t)$ is expected to become less accurate as $m'\sigma$ exceeds 1 because, correspondingly, the state $\bar{x} \simeq \hat{x}$ is no longer metastable ([23], Sec. S2B). For slow and fast migration, $H(t) \simeq H(0)$ for a rather long time, whereas $H(t)$ rapidly decreases in time for intermediate values of the migration rate. For a fixed time,
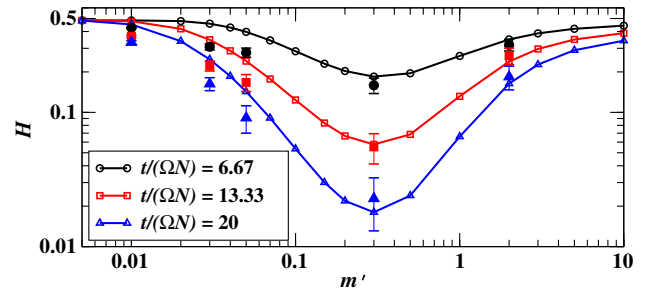

FIG. 4 (color online). Dependence of the global heterozygosity H on the migration rate m' at various times, for a subdivided population with $\Omega = 100$, $N = 30$, $s' = 1$, and $x_* = 1/2$: the prediction of the approximation described in the text (solid lines) is compared with the results of simulations of the WF model (symbols with error bars).

and as a function of m', instead, H has a minimum at $m' \simeq m'_{\min}$, indicating that the global biodiversity can be enhanced upon increasing migration [31]. Our predictions agree rather well with the results of simulations, apart from, as expected, $m' \lesssim 1/\sigma \simeq 0.03$. A similar study of both H for different values of the parameters and h [23] highlights a nonmonotonic dependence on m' whenever the corresponding T_{fix} develops a minimum.

Conclusions.—Focusing on the Island model [29], we have shown that the mean fixation time of a subdivided population can become a nonmonotonic function of the migration rate m in the presence of balancing selection, an evolutionary mechanism which promotes the coexistence of different genetic traits within the same populations. The emergence of a minimum depends on both the selection strength $\sigma \equiv s\Omega N$ exceeding a threshold and on the frequency x_* of coexistence which is promoted by the selection. While the MFT increases upon decreasing m because of the slowing down in the migration dynamics, its possible increase for sufficiently large m has a less intuitive explanation. *A posteriori*, this is due to the formation of a metastable state, the "life time" of which might increase upon increasing the migration rate. Our result extends beyond population genetics: it carries over to any other evolutionary model whose dynamics has an internal attractive equilibrium (coexistence) in addition to absorbing states (specialized states). Moreover, these features should also appear in subdivided populations with more complex migration or spatial [32] structures. It would be interesting to understand whether the features discussed here also emerge by introducing balancing selection in those population models for which subdivision induces a bifurcation [33], a phase transition [34], or a maximum in some characteristic times of the dynamics [35]. The approach presented here for describing the dynamics of the entire population via an effective Langevin equation can be generically applied to any collective dynamics in which fast local variables are influenced by slow, global, "mean-field-like" quantities. In this respect, it extends to

transient properties the self-consistent mean-field-like approximations typically used in statistical physics to investigate the stationary properties of nonequilibrium processes [36].

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