



Fixation and absorption in a fluctuating environment

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ABSTRACT

A fundamental problem in the fields of population genetics, evolution, and community ecology, is the fate of a single mutant, or invader, introduced in a finite population of wild types. For a fixed-size community of N individuals, with Markovian, zero-sum dynamics driven by stochastic birth-death events, the mutant population eventually reaches either fixation or extinction. The classical analysis, provided by Kimura and his coworkers, is focused on the neutral case, [where the dynamics is only due to demographic stochasticity (drift)], and on *time-independent* selective forces (deleterious/beneficial mutation). However, both theoretical arguments and empirical analyses suggest that in many cases the selective forces fluctuate in time (temporal environmental stochasticity). Here we consider a generic model for a system with demographic noise and fluctuating selection. Our system is characterized by the time-averaged (log)-fitness s_0 and zero-mean fitness fluctuations. These fluctuations, in turn, are parameterized by their amplitude γ and their correlation time δ . We provide asymptotic (large N) formulas for the chance of fixation, the mean time to fixation and the mean time to absorption. Our expressions interpolate correctly between the constant selection limit $\gamma \rightarrow 0$ and the time-averaged neutral case $s_0 = 0$.

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1. Introduction

Complex systems are usually affected by both deterministic and stochastic forces, and a reliable assessment of their relative importance is, in many cases, a difficult task. The neutralist-selectionist debate (Nei, 2005) in the field of molecular biology is a typical example: selectionists believe that deterministic selection is the dominant mechanism that shapes the genetic polymorphism in a population, while neutralists stress the effect of demographic stochasticity (drift). The neutral model (with some modifications, like spatial structure) was imported to ecology by Hubbell (2001) and Leigh (2007), and the arguments about the relative importance of deterministic (niche) vs. stochastic (neutral) factors have filled many pages of the ecological literature ever since (McGill et al., 2006; Ricklefs and Renner, 2012; Rosindell et al., 2011).

In these debates, the effect of deterministic forces is usually contrasted with *demographic stochasticity*, that is, those random aspects of dynamics that affect the reproductive success of individuals in an *uncorrelated* (between individuals and over time) manner. On the other hand, the selective/niche forces are assumed to affect an entire population (species, allele, phenotype, strain) and to be independent of time.

Recently, many authors have considered another possibility: fluctuating selective pressure, or temporal environmental stochasticity (Ashcroft et al., 2014; Assaf et al., 2013; Cvijović et al., 2015; Hidalgo et al., 2017; Kalyuzhny et al., 2015; Lande et al., 2003; Wienand et al., 2017). Time-varying environment may affect the selective advantage of an entire population, adding to the model a force which is correlated among individuals of the same type but changes randomly through time.

There are several good reasons to engage in models that allow for temporal environmental stochasticity. A-priori, it is difficult to imagine a mutation or a trait which are purely beneficial. An increase of body mass, for example, may have many beneficial aspects but it exposes the individual to an increased pressure when the environment deteriorates (e.g., during a drought). These trade-offs are quite ubiquitous in nature (Cvijović et al., 2015) so one expects environmental variations to change the relative fitness of species and strains. Moreover, the per-generation variations in population size due to environmental stochasticity are $\mathcal{O}(n)$ (where n is the size of the population), while demographic stochasticity generates $\mathcal{O}(\sqrt{n})$ noise. Therefore, for a population of a reasonable size environmental stochasticity should be the dominant process (Lande et al., 2003).

Empirically, the fluctuations in population size that were measured in a wide variety of systems scale in many cases like n , and in almost any case were found to be much larger than

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$\sqrt{n}$ (Chisholm et al., 2014; Kalyuzhny et al., 2014a; 2014b; Leigh, 2007). Measurements of the selection coefficients for different characters (or variants) of a single species also indicate that selective forces are time dependent, often changing their direction (Bell, 2010). Consequently, the need to extend the theory in order to incorporate environmental stochasticity (also known as temporal niches, fluctuating selection, alternating selective pressure and so on) received a considerable attention during the last years (Cvijović et al., 2015; Danino et al., 2017; 2018; 2016; Fung et al., 2016; Hidalgo et al., 2017; Kalyuzhny et al., 2015; Kessler et al., 2016; Kessler and Shnerb, 2014; Sæther and Engen, 2015).

In this paper we would like to address a simple question, which is also one of the cornerstones of the theories of population genetics and community dynamics: the fate of a single mutant in a finite size community. This question has been addressed long ago for the cases with pure demographic stochasticity and constant selection (Crow et al., 1970; Ewens, 2012), and we would like to extend the theory to include random selective forces. To do that, we consider a simple and generic model for a community of N individuals, affected by selection, demographic noise and temporal environmental stochasticity. Using asymptotic (large N) techniques we obtained expressions for three quantities:

1. The chance of fixation for a single mutant, $\Pi(n=1)$, which is the probability that the system ends up in the absorbing state with N mutants.
2. The average time to absorption (fixation or loss) $T_A(n=1)$, the expected time taken to reach any one of the absorbing states, given that the system is started with a single mutant/invaser.
3. The average fixation time $T_f(n=1)$, i.e. the mean time between the introduction of the mutant/invaser and the fixation of the system by its lineage, *conditioned on fixation*.

In the above definitions, average is taken over both histories and initial conditions. For example, the average time to absorption is defined as $T_A = (T_A^+ + T_A^-)/2$, where T_A^+ (T_A^-) are the average time to absorption when at $t=0$ the environment was in the plus (minus) state, i.e., when the fitness of the mutant type is higher (lower) than that of the wild type (see formal definitions below).

2. Methods

We consider a community of N individuals, where at $t=0$ one individual is a mutant or invader and all others are wild types. Our model is inspired by the standard competitive Lotka–Volterra dynamics, where two species compete for the same resource. In its individual based version one may consider two (randomly picked) individuals that fight for a piece of food, say, the winner reproduces and the loser dies. In each elementary step of our Moran process two individuals (i and j) are chosen at random for such a duel. If both individuals belong to the same species, the result of the duel does not affect the abundance. In case of an interspecific duel, the chance of an individual to win depends on its relative fitness. The mutant and its descendants have logarithmic fitness s_μ and wild type individuals have fitness s_w . A mutant type wins a duel against a wild type with probability,

$$P_\mu = \frac{1}{2} + \frac{s_\mu - s_w}{4}, \quad (1)$$

where the chance of the wild type to win is $1 - P_\mu$. Since P_μ depends only on $s_\mu - s_w$, we can take, without loss of generality, $s_w = 0$ and denote s_μ (the logarithmic relative fitness of the mutant) simply by s . Time is measured in units of generations, where a generation is defined as N elementary duels.

Under temporal environmental stochasticity s is a function of time and we assume that it takes the form

$$s(t) = s_0 + \eta(t), \quad (2)$$

where s_0 is the time-averaged (log)-fitness difference between the mutant lineage and the wild types while the (zero mean) variable $\eta(t)$ reflects the effect of environmental variations. These environmental fluctuations are characterized by two quantities: their amplitude γ and their correlation time (measured in units of a generation) δ .

Following Danino et al. (2018) and Hidalgo et al. (2017) we model temporal environmental stochasticity by dichotomous (telegraphic) noise, so $\eta(t)$ may take two values, either $(+\gamma)$ or $(-\gamma)$. After each elementary duel the chance of the environment to stay in the same state is $1 - 1/(\delta N)$, while its chance to flip (i.e., $\pm\gamma \rightarrow \mp\gamma$) is $1/(\delta N)$. Both white Gaussian noise and white Poisson noise can be recovered from the dichotomous noise by taking suitable limits (Ridolfi et al., 2011), so the results obtained here are quite generic. A detailed description of the process, including the transition probabilities and the form of the corresponding backward Kolomogorov equation (BKE), is given in Appendix A.

This process is very similar to the one presented for the same problem in Ashcroft et al. (2014), who provided closed-form expressions for fixation times and the fixation probability using the theory of Markov chains and the elementary transition rates. Here we would like to obtain explicit and simple expressions for these quantities in the large- N limit, which is the relevant regime in most of the realistic applications.

To do that, we implement the techniques we have developed recently in Danino et al. (2018) (the main results that are relevant to this work are summarized in Appendix A). We used the continuum approximation, where the number of mutants n is replaced by their fraction $x = n/N$ and quantities like $\Pi(x + 1/N)$ are expanded to second order in $1/N$. The relevant BKEs emerge as two coupled, second order differential equations [such as Eqs. (A.3) below]. Using a dominant balance analysis we can show that, in the large N limit, these BKEs may be reduced to a single second order differential equation. This procedure is demonstrated in Appendix A for the time to absorption $T_A \equiv (T_A^+ + T_A^-)/2$: instead of having two coupled equations for $T_A^\pm$, we obtain a single equation for T_A .

Using that, and the standard techniques to obtain Π , T_A and T_f (Redner, 2001), we can write down, for each case, the relevant equation with the appropriate boundary conditions, as detailed in the appendices below [Eqs. (B.1), (C.1) and the pair of Eqs. (D.1) and (D.2)]. In all three cases the set of equations may be solved quite easily using integration factor, but the results are given in terms of nested integrals over hypergeometric functions that do not provide a transparent analytic picture. To overcome this difficulty, we have calculated the leading terms in the large N asymptotic series (Table 1).

The details of these calculations are given in the three appendices Appendix B–D. In the next section we present and discuss the bottom-lines results in terms of s_0 (the time-averaged mutant fitness), N (that sets the scale of demographic noise, which is $1/N$), $g = \gamma^2\delta/2$, the effective strength of environmental stochasticity, $\alpha = s_0/g$, the ratio between deterministic and stochastic selective forces and $G \equiv Ng$, the ratio between the environmental and the demographic stochasticity (see glossary).

Our operational definition of a “generation” is N duels. To use the formulas presented below with a different definition of a generation time, say, AN duels, one should stick to the definition of δ as the persistence time of the environment in units of N . For example, if the weather changes every 100 duels and the size of the community is $N = 1000$, $\delta = 0.1$ no matter what A is. Doing that, the formulas obtained here may be used as long as T_f and T_A are divided by A .

As explained, the results presented here are the outcomes of large- N asymptotic analysis. In particular, the asymptotic matching technique used in the appendices assumes that the demographic

Table 1
Glossary.

Term	Description
N	number of individuals in the community.
n	number of mutant type individuals ($N - n$ wild type).
x	fraction of mutants, $x = n/N$. ($1 - x$ is the fraction of wild type)
s_0	time-averaged fitness of the mutant.
δ	correlation time of the environment, measured in generations.
γ	the amplitude of the fitness fluctuations.
$g \equiv \delta\gamma^2/2$	strength of environmental stochasticity.
$\alpha \equiv s_0/g$	the ratio between the constant selective force and the strength of temporal environmental stochasticity
$G \equiv N\delta\gamma^2/2$	scaled environmental stochasticity.
$T_A(n=1)$	mean persistence time for a two species system, if at $t=0$ there is only a single mutant ($n=1$). Average (for this and other quantities) is taken over histories and initial conditions.
$\Pi(n=1)$	mean (over initial conditions) chance of fixation for a single mutant.
$T_f(n=1)$	mean time to fixation for a single mutant.

noise terms $1/N$ is negligible, with respect to $gx(1-x)$, as long as x is not too close to zero or one. Accordingly, our analysis does not cover the limit in which the environmental stochasticity vanishes, i.e., $g=0$: the value of g may be vanishingly small as long as

$$G = Ng \gg 1. \quad (3)$$

This implies that we cannot recover the purely demographic limit where both g and s_0 vanishes. However for any finite s_0 our expressions converge to the correct answer even in the limit $g \rightarrow 0$ as long as $G \gg 1$ (see discussion below).

In the following section we compare our results with numerical solutions of the backward Kolomogorov equations that involve simple inversion of the $2N \times 2N$ transition matrix, as detailed in the first appendix of Danino et al. (2018). Using the sparsity of the relevant matrices we were able to reach system sizes up to $N = 10^6$.

3. Results

3.1. The chance of fixation $\Pi(n=1)$

For pure demographic noise (neutral system, $s_0 = 0$ and $g = 0$) the chance of a mutant to win is known to be

$$\Pi_{g=s_0=0}(n=1) = \frac{1}{N}.$$

This result is trivial: since all individuals are symmetric, the chance of the lineage of each of them to reach fixation must be equal.

Under constant selection s_0 (still $g=0$) the chance of a single advantageous mutant to reach fixation is

$$\Pi_{g=0}(n=1) = \frac{1 - e^{-s_0}}{1 - e^{-Ns_0}} \approx 1 - e^{-s_0} \approx s_0, \quad (4)$$

where the first approximation is the strong selection ($Ns_0 \gg 1$) limit, and the second corresponds to the large N , small s_0 , limit.

The intuitive argument behind Eq. (4) is as follows Desai et al. (2007): the mutant lineage starts to feel the deterministic bias only at $n_c(s_0, g=0) \sim 1/s_0$, where its abundance grows on average by one individual per generation. Below n_c the process is dominated by the demographic noise. Therefore, the chance of fixation is actually the chance of the lineage of a single mutant to reach n_c under pure demographic noise

$$\Pi_{g=0}(n=1) \approx \frac{1}{n_c(s_0, g=0)} \approx s_0.$$

The condition for strong selection is translated to $N \gg n_c$.

Now let us turn to our results. For a single mutant where g is finite and $G = gN \gg 1$, the chance of fixation (calculated in Appendix B) is,

$$\Pi(n=1) \sim \frac{1 - \frac{1}{(1+g)^{s_0/g}}}{1 - G^{-2s_0/g}}. \quad (5)$$

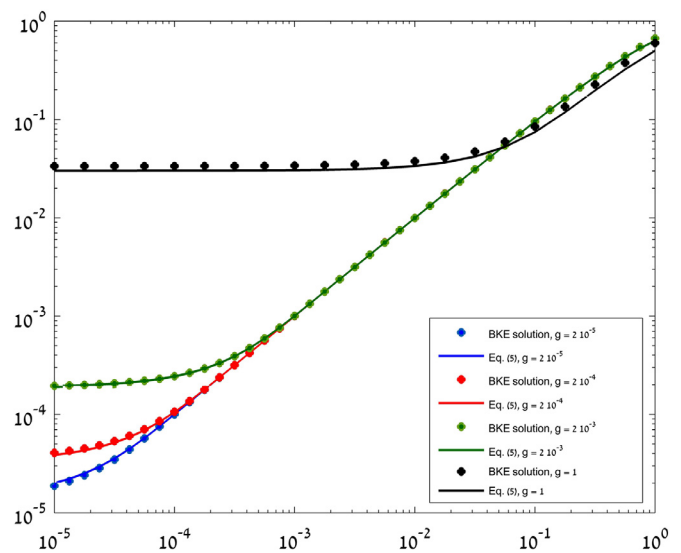


Fig. 1. $\Pi(n=1)$ vs. s_0 for different values of G . $\Pi(n=1)$, as obtained from numerical solutions of the discrete backward Kolomogorov equation (open circles), and the large G approximation, Eq. (5) (full lines), are plotted against s_0 for $N = 10^5$ and different values of $G = N\gamma^2\delta/2$ (see legend). The fit is almost perfect, with only slight deviations (where the analytic formula still have the same shape) at $g = 2 \cdot 10^{-5}$, $G = 2$ (see Eq. (3)) and at $g = 1$, $G = 10^5$ (where the continuum approximation becomes problematic). For small values of s_0 , the chance of fixation grows as g increases. On the contrary, for large values of s_0 the chance of fixation decreases when g increases, as explained in the text.

As demonstrated in Fig. 1, this formula matches almost perfectly, without any fitting parameters, the numerical solutions of the discrete, exact BKE. Slight deviations are observed at $G = 2$, where the asymptotic matching analysis becomes problematic. When the noise is very large ($g = 1$) tiny deviations are observed again, here the reason is that the continuum approximation fails close to $x = 0$ and $x = 1$ (for more details see Fig. B.5 at the end of Appendix B and the discussion section).

The formula for $\Pi(n=1)$, given in Eq. (5) has the following features:

- For $s_0 = 0$, g finite, Eq. (5) converges to the expression suggested in Cvijović et al. (2015), namely,

$$\Pi(n=1) = \frac{\ln(1+g)}{2\ln(G)}. \quad (6)$$

In this case the chance of fixation *increases* with g . To understand why, note that in the large N limit under environmental stochasticity the abundance preforms a random walk along the $\log(x/[1-x])$ axis, so the chance of fixation is much larger than

$1/N$ (the chance in the purely demographic case) since the mutant lineage may conquer the whole system in $\mathcal{O}(\log N)$ steps.

- On the other hand, when s_0 and g are finite but $N \rightarrow \infty$, the denominator in Eq. (5) is unity and $\Pi(n=1)$ is a monotonously decreasing function of g . This has to do with the value of n_c , below which the system is dominated by noise and above it the growth is deterministic and fixation occurs almost surely. While for a system without environmental variations $n_c(s_0, g=0) = 1/s_0$, when $g > 0$ (Cvijović et al., 2015; Danino et al., 2017)

$$n_c(s_0, g) = \frac{e^{g/s_0} - 1}{g}. \quad (7)$$

This expression converges to $1/s_0$ when $g=0$, but increases exponentially with g so it is more difficult for the mutant lineage to enter the deterministic growth zone.

- Accordingly, for any finite value of N and s_0 there is a critical strength of environmental stochasticity, g_c , above which the chance of fixation increases with g . At g_c $d\Pi_{n=1}/dg$ vanishes: this yields a transcendental equation for the critical noise level. While we cannot solve for g_c in general, numerical solutions seem to indicate that $g_c \approx s_0 \ln(N)$. Up to logarithmic corrections one may obtain this expression from the condition $N = n_c(s_0, g)$, so the system is close to its time-averaged neutral limit (in the sense used in Kalyuzhny et al. (2015)) when $N < n_c$ and is in the strong selection regime for $N > n_c$.

This outcome may have interesting implications to the theory of bet-hedging strategies, phenotypic plasticity and related phenomena (Kussell and Leibler, 2005; Philippi and Seger, 1989). Bet-hedging allows species and individuals to cope with changing environmental conditions by decreasing their fitness in their typical conditions in exchange to increased fitness under stressful conditions. If such a strategy happens to increase the time average log fitness s_0 then of course it reduces the chance of extinction. However, if the only effect of these strategies is to reduce the variance in fitness γ while keeping s_0 fixed, they will be beneficial for a species in a zero-sum competitive community only in the strong selection limit.

- For deleterious mutations ($s_0 < 0$), Eq. (5) predicts that the chance of fixation decays with N like a power-law, $(Ng)^{-2|s_0|/g}$. Numerically, we discovered that this result holds only when $s_0 \ll \gamma$. Curiously, this result is identical with the one obtained recently by Assaf et al. (2013).
- As discussed towards the end of the methods section, the case $g=0$ is problematic since the condition $G \gg 1$ is no longer holds. Still, as long as s_0 is finite, taking the limit $g \rightarrow 0$ is legitimate if G is still large, e.g., $g \sim 1/\sqrt{N}$, as $N \rightarrow \infty$. In this case Eq. (5) converges to the large N limit of a system with constant selection, $1 - e^{-s_0} \approx s_0$, as needed.
- As explained above, the pure demographic noise result $\Pi = 1/N$ cannot emerge from Eq. (5) by taking both s_0 and g to zero. Since N should be taken to infinity first, the chance of fixation in this case vanishes. Under constant selection the chance of fixation is finite even in the infinite N limit (this is why we obtained the correct result in that case), but not under pure demographic stochasticity. However, in almost any realistic scenario either s_0 or g (and perhaps both) are larger than $1/N$. If both s_0 and g are vanishingly small one may simply use the results for the pure demographic scenario since the selective forces are only tiny perturbation. This point is demonstrated in Fig. 2.

3.2. The time to absorption T_A

The time to absorption T_A is the average time from the event of mutation/invasion until the system becomes homogenous again,

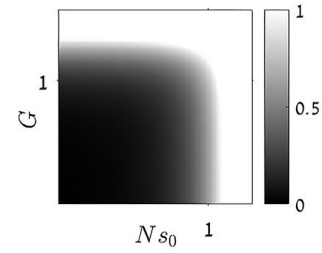


Fig. 2. The value of $N\Pi(n=1) - 1$ in the $Ns_0 - G$ plane. Under purely demographic stochasticity $\Pi(n=1) = 1/N$, so the quantity $N\Pi(n=1) - 1$ is a measure of the effective distance from the demographic limit. Here this quantity, obtained from numerical solution of the BKE with $N = 1000$, is plotted in the $Ns_0 - G$ plane (for both axes logarithmic scale has been used) where the grey level indicates its value. As expected, when both Ns_0 and G are smaller than one the system is close to the purely demographic regime.

i.e., until the mutant lineage either goes extinct or reaches fixation. In Appendix C we show that the asymptotic expression for this quantity is,

$$T_A(n=1) = \left(\frac{\ln(G)}{s_0} - \frac{G^{2s_0/g} \beta_2 - \beta_1}{G^{2s_0/g} - 1} \right) \left(1 - \frac{1}{(1+g)^{s_0/g}} \right) - \frac{1}{g(1+g)^{s_0/g}} \int_0^g \frac{\ln(z) dz}{(1+z)^{1-s_0/g}}, \quad (8)$$

where

$$\beta_1 \equiv \frac{1}{s_0} [H(\alpha) + \pi \cot(\pi \alpha) + \ln(G)],$$

$$\beta_2 \equiv \frac{1}{s_0} [-H(-\alpha) + \pi \cot(\pi \alpha) - \ln(G)],$$

and $H(x)$ is the Harmonic number. This expression becomes simpler when N approaches infinity, where it takes the form,

$$T_A(n=1) \sim \frac{2}{s_0} \left(1 - \frac{1}{(1+g)^{s_0/g}} \right) \ln(N). \quad (9)$$

However, the rate of convergence of Eqs. (8) and (9) is slow, and when we tested our results against the numerical solutions of the BKE at $N = 10^5$ (Fig. 3), we implemented Eq. (8).

- When $g \rightarrow 0$ Eq. (8) converges to

$$T_A(n=1) \sim 2(1 - e^{-s_0}) \ln(N)/s_0 \approx 2 \ln(N). \quad (10)$$

This is the correct limit for a singleton without environmental stochasticity (Ewens, 2012).

- On the other hand when $s_0 \rightarrow 0$ (9) yields

$$T_A(n=1) \sim 2 \frac{\ln(1+g)}{g} \ln(N), \quad (11)$$

which it the result obtained in Danino et al. (2018). The simple expression (9) interpolates between these two limits. Unlike the fixation time considered below, T_A is always logarithmic in N , hence the interpolation between these two limits involves only the prefactor.

3.3. The time to fixation T_f

The fixation time is the average time between mutation and fixation, when the average is taken over all the trajectories that start at $n=1$ and end up at $n=N$. In Appendix D we show that,

$$T_f(n=1) \sim 2 \left(\frac{[1 + G^{2s_0/g}] \ln(G)}{s_0 [G^{2s_0/g} - 1]} - \frac{\pi \cot(\pi s_0/g)}{s_0} + \frac{H(s_0/g) + G^{2s_0/g} H(-s_0/g)}{s_0 [G^{2s_0/g} - 1]} \right). \quad (12)$$

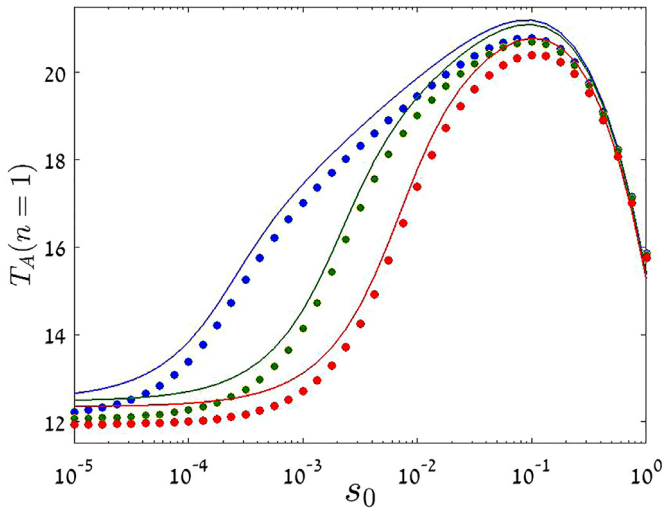


Fig. 3. $T_A(n=1)$ vs. s_0 . The time to absorption of a single mutant, as obtained from numerical solutions of the discrete backward Kolomogorov equation (filled circles), is compared with the predictions of Eq. (8) (lines). The results are plotted against s_0 for $N = 10^5$, $\delta = 0.09$, and the values of γ are 0.1 (blue), 0.4 (green) and 0.8 (red), so g runs between $4.5 \cdot 10^{-4}$ and $2.9 \cdot 10^{-2}$. Since the extinction times are of order one, the large N behavior of T_A is determined by $\Pi \cdot T_f$. Accordingly T_A first increases with s_0 (since Π increases) and then decreases (when the dominant effect is the decrease of T_f with s_0). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

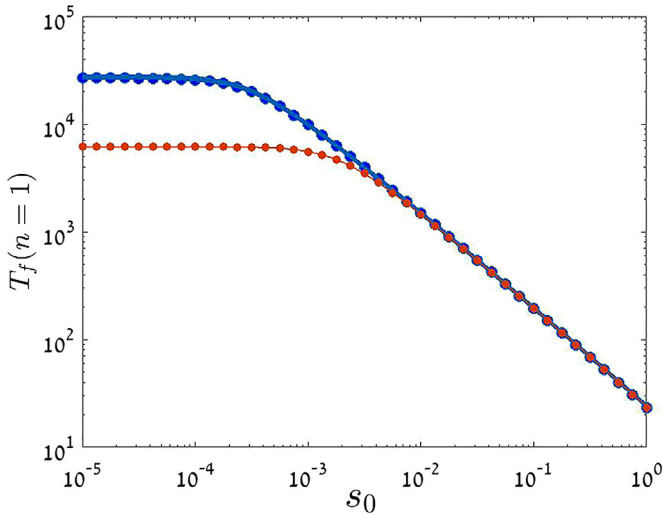


Fig. 4. $T_f(n=1)$ vs. s_0 . The time to fixation, as obtained from numerical solutions of the discrete backward Kolomogorov equation (filled circles), is compared with the predictions of Eq. (12) (full lines), both plotted against s_0 for $N = 10^5$, $\gamma = 0.1$ and $\delta = 0.09$ ($g = 4.5 \cdot 10^{-4}$, blue) and $\delta = 0.9$ ($g = 4.5 \cdot 10^{-3}$, brown). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Although this expression has a singular point at $s_0 = g$, the curve is smooth out of a region of width $1/N$ around the singular point, so this singularity is negligible in the large N limit. Fig. 4 depicts the fit of (12) to the numerical solution of the discrete BKE.

- As $N \rightarrow \infty$ when s_0 and g are kept fixed, Eq. (12) yields,

$$T_f(n=1) \sim \frac{2}{|s_0|} \ln(N), \quad (13)$$

as expected. In this limit the random walk in the log-abundance space, associated with the environmental stochasticity, may be neglected with respect to the constant bias.

- On the other hand, for fixed N and g when s_0 vanishes,

$$T_f(n=1) \sim \frac{2}{3g} \ln^2(gN). \quad (14)$$

Note that Eq. (14) is a result of a third order expansion of (12), where the lower order terms cancel out. For fixed g , the large N approximation Eq. (13) is valid (as in the case of Π) as long as $G^{2s_0/g} \gg 1$, i.e., as long as $s_0 \ln(gN)/g > 1$, or simply $N \gg n_c(s_0, g)$.

- T_f is a symmetric function of s_0 (this was shown, for a model without environmental stochasticity, in Taylor et al. (2006). Eq. (12) implies that this feature holds under fluctuating selection). T_f peaks at $s_0 = 0$.

4. Discussion

Through this paper we have calculated and analyzed three fundamental quantities that have to do with the fate of a mutant, or an immigrant, in a community of size N under the effect of selection, demographic stochasticity (drift) and environmental variations. These quantities: the chance of fixation, the time to absorption and the time to fixation, govern the dynamics of evolution for a community with fixed mutation rate, as explained in Cvijović et al. (2015) and Danino et al. (2017). We have focused our discussion on the fate of a single mutant/invaser; other quantities, like the maximum time to absorption (for example, in the absence of selection it is clear that the maximum time to absorption occurs when the community is divided equally between the two species, $n(t=0) = N/2$) were calculated in Danino et al. (2018). In fact, the same analytic methods we have used in the appendices may be utilized to calculate the relevant quantities for any value of n (not only a single mutant) given N , g and s_0 .

Our analysis is based on equations for the average quantities, where average is taken over both histories and initial conditions. These equations are similar to those obtained using the standard diffusion approximation (Karlin and Taylor, 1981), but there are a few technical differences. Our treatment begins with the introduction of an exact backward Kolomogorov equation, followed by transition to the continuum, dominant balance analysis that allows us to neglect a few terms and then by the calculation of the large N asymptotic behavior. This methodology allows for better identification of the limits of our theory, and we would like to emphasize three of these limiting factors:

- "Single sweep" fixation:** In our results, the effect of environmental noise is expressed by a single parameter $g = \gamma^2 \delta / 2$. This parameter may be considered as the diffusion constant in the log-abundance space: If $x = n/N$ is the fraction of mutants and $\dot{x} = \pm \gamma x(1-x)$, the system performs an unbiased random walk on the $z = \ln[x/(1-x)]$ axis with an effective "diffusion constant" $\gamma^2 \delta$. Clearly, this is not the case when the fixation takes place during δ generations, i.e., when $\delta > \ln(N)/(\gamma + s)$. In such a case the single parameter (g) scaling breaks down. This possibility has been discussed in Cvijović et al. (2015) and Danino et al. (2018), but appears to be less interesting as it describes an isolated catastrophe instead of the accumulation of environmental variations over time.
- Breakdown of the continuum approximation:** When the quantities considered here change their values abruptly between n and $n+1$ (this happens, usually, close to $n=0$ or $n=N$) the transition to the continuum may fail and one should consider the original difference equations instead of the differential equations. For a detailed discussion of this problem (in different system) and a WKB recipe suggested for that case, see Kessler and Shnerb (2007). In Fig. 1 above

this problem manifests itself in the $g = 1$, $G = 2 \cdot 10^5$ (very strong stochasticity) case.

Assaf et al. (2013) have considered a prisoner dilemma game that may be mapped into the negative s_0 case of our system, and implemented the WKB technique. To do that, they introduced reflecting boundary conditions at the initial value of x , and exploit the relationship between the mean fixation time and the probability of fixation in this modified system. As a result, their approach allows them to obtain the leading exponential behavior, but not the prefactors.

3. **Breakdown of the asymptotic matching:** As discussed above, our asymptotic matching analysis is based on the assumption that $G \gg 1$. If this is not the case, one cannot identify the inner, middle and outer regimes as done in the appendices. In Fig. 1 we have seen, indeed, that when $G = 2$ the deviations of our theory from the exact numerical results are identifiable.

One aspect of community dynamics that we did not take into account is a stabilizing mechanism which is similar to the one known as the storage effect (Chesson and Warner, 1981). For a system with storage, the environmental variations stabilizes the coexistence state (in the absence of selection, at $n = N/2$), thus facilitating the invasion of new species or a mutant (and increasing the chance of fixation (Danino et al., 2017)). Quantities like the time to fixation, or even the chance of fixation per se, may be less relevant for systems with storage effect. In these systems, when a mutant invades it typically reaches the coexistence state and stay around for a long time (about $N^{1/\delta}$ generations, see Danino et al., 2018; Hidalgo et al., 2017), only then one of the species goes extinct. Accordingly, for most purposes the relevant quantity under storage is not the chance of fixation but the chance of establishment (Danino et al., 2017). We hope to address this question in subsequent publication.

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Appendix A. Technical definitions and the Backward Kolomogorov equation

Our Moran process under dichotomous stochasticity is fully characterized by twelve transition rates. In each elementary step the mutant population may stay the same or grow/shrink by one individual. At the same time the environment may switch from its (+) state (where the chance of the mutant to win a duel is $1/2 + s_0/4 + \gamma/4$) to a (−) state (where the winning probability is $1/2 + s_0/4 - \gamma/4$) and vice versa. Defining $x = n/N$ as the mutant fraction in the population, the transition probabilities W are given by,

$$\begin{aligned} W_{n \rightarrow n+1}^{++} &= W_{n \rightarrow n-1}^{--} = 2x(1-x) \left(\frac{1}{2} + \frac{s_0}{4} + \frac{\gamma}{4} \right) \left(1 - \frac{1}{\delta N} \right) \\ W_{n \rightarrow n+1}^{--} &= W_{n \rightarrow n-1}^{++} = 2x(1-x) \left(\frac{1}{2} + \frac{s_0}{4} - \frac{\gamma}{4} \right) \left(1 - \frac{1}{\delta N} \right) \\ W_{n \rightarrow n+1}^{+-} &= W_{n \rightarrow n-1}^{-+} = 2x(1-x) \left(\frac{1}{2} + \frac{s_0}{4} - \frac{\gamma}{4} \right) \frac{1}{\delta N} \\ W_{n \rightarrow n+1}^{-+} &= W_{n \rightarrow n-1}^{+-} = 2x(1-x) \left(\frac{1}{2} + \frac{s_0}{4} + \frac{\gamma}{4} \right) \frac{1}{\delta N} \\ W_{n \rightarrow n}^{++} &= W_{n \rightarrow n}^{--} = \left(1 - \frac{1}{\delta N} \right) [1 - 2x(1-x)] \\ W_{n \rightarrow n}^{+-} &= W_{n \rightarrow n}^{-+} = \frac{1}{\delta N} [1 - 2x(1-x)] \end{aligned} \quad (\text{A.1})$$

where $W_{n \rightarrow n+1}^{++}$ is the probability to increase the mutant population by one individual while staying in the plus environment, while $W_{n \rightarrow n+1}^{+-}$ is the chance that the environment switches from plus to minus and after this switch the mutant population grew.

After each duel time is incremented by $1/N$, so the BKE for the time to absorption, say, takes the form,

$$\begin{aligned} T_A^+(n) &= \frac{1}{N} + W_{n \rightarrow n+1}^{++} T_A^+(n+1) + W_{n \rightarrow n-1}^{++} T_A^+(n-1) + W_{n \rightarrow n}^{++} T_A^+(n) \\ &\quad + W_{n \rightarrow n-1}^{+-} T_A^-(n-1) + W_{n \rightarrow n+1}^{+-} T_A^-(n+1) + W_{n \rightarrow n}^{+-} T_A^-(n) \\ T_A^-(n) &= \frac{1}{N} + W_{n \rightarrow n-1}^{--} T_A^-(n-1) + W_{n \rightarrow n+1}^{--} T_A^-(n+1) + W_{n \rightarrow n}^{--} T_A^-(n) \\ &\quad + W_{n \rightarrow n+1}^{-+} T_A^+(n+1) + W_{n \rightarrow n-1}^{-+} T_A^+(n-1) + W_{n \rightarrow n}^{-+} T_A^+(n) \end{aligned} \quad (\text{A.2})$$

Defining $T_A(n) = [T_A^+(n) + T_A^-(n)]/2$, $\Delta(n) = [T_A^+(n) - T_A^-(n)]/2$, moving to the continuum limit and expanding $T(x \pm 1/N)$ to the second order in a Taylor series one finds:

$$\begin{aligned} \frac{2\Delta}{\delta N x(1-x)} &= \left(1 - \frac{2}{\delta N} \right) \left[\frac{\gamma}{N} T_A' + \frac{\Delta''}{N^2} + s_0 \frac{\Delta'}{N} \right] \\ &\quad - \frac{1}{x(1-x)} = \frac{T_A''}{N} + \gamma \Delta' + s_0 T_A'. \end{aligned} \quad (\text{A.3})$$

Where primes indicate a derivative with respect to x . If δ is kept fixed (say, $1/10$ of a generation) and N increases, $\delta N \gg 1$ and

$$\begin{aligned} \frac{2\Delta}{\delta x(1-x)} &= \gamma T_A' + \frac{\Delta''}{N} + s_0 \Delta' \\ &\quad - \frac{1}{x(1-x)} = \frac{T_A''}{N} + \gamma \Delta' + s_0 T_A'. \end{aligned} \quad (\text{A.4})$$

Neglecting the Δ''/N and the Δ' terms in the upper equation, solving for Δ in terms of T_A' , $\Delta = \gamma \delta x(1-x) T_A'/2$, and plugging the expression for Δ' into the lower equation, one obtains,

$$-\frac{1}{x(1-x)} = \left[\frac{1}{N} + g x(1-x) \right] T_A'' + [s_0 + g(1-2x)] T_A', \quad (\text{A.5})$$

which is exactly Eq. (C.1).

The dominant balance argument that leads to the neglect of the Δ''/N and the Δ' terms in the upper equation was motivated by a term by term analysis of the numerical solutions of the discrete BKE (A.2). The argument is self consistent in the middle regime: extracting Δ from Eq. (C.13) and calculating the relevant terms, the two neglected terms were found to be subdominant in the $G \rightarrow \infty$ limit.

Apparently, this has to be the case. First, if the $\gamma s'$ term is subdominant, then $\Delta = 0$ and the effect of environmental stochasticity vanishes. Therefore, the only question is, which term balances the $\gamma s'$ in the large N limit. Clearly, if the balancing term is the Δ' environmental stochasticity only renormalizes the value of s_0 , while the Δ'' leads to a renormalization of the strength of the demographic noise. Accordingly, and in agreement with the outcomes of our numerical solutions, the dominant balance argument makes sense.

Appendix B. Large- N asymptotics for the chance of fixation Π

Defining $x = n/N$ and using the results of Danino et al. (2018) (Appendix C), the chance of fixation $\Pi(x)$ satisfies (Redner, 2001),

$$\begin{aligned} \left(\frac{1}{N} + g x(1-x) \right) \Pi''(x) + (s_0 + g(1-2x)) \Pi'(x) &= 0, \\ \Pi(0) &= 0 \quad \Pi(1) = 1. \end{aligned} \quad (\text{B.1})$$

To calculate the large N asymptotic of Π , we will solve (B.1) in three different regions:

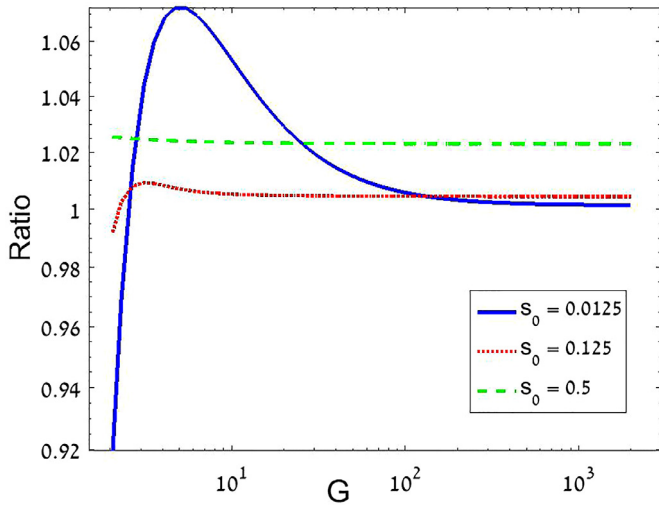


Fig. B1. $\Pi(n=1)$, as obtained from numerical solutions of the discrete backward Kolomogorov equation, divided by the large G approximation, Eq. (B.14), for different values of s_0 as function of G . As G gets smaller the approximation (B.14) becomes less accurate. The large G ratio is closer to one when s_0 is small. When s_0 is large, the continuum approximation at small values of n is not accurate, as discussed in the main text (see also the discussion section).

1. The inner region $0 \leq x < 1$. In this region the number of individuals may be small [even for large N , $n = Nx$ may be $\mathcal{O}(1)$] and demographic noise affects the system. The relevant equation for $\Pi_{in}(x)$ is obtained from (B.1) by replacing $1-x$ and $1-2x$ by unity, and is subject to a single boundary condition at zero,

$$\left(\frac{1}{N} + gx\right)\Pi''_{in}(x) + (s_0 + g)\Pi'_{in}(x) = 0, \quad \Pi_{in}(0) = 0. \quad (\text{B.2})$$

Using an integrating factor one may easily show that,

$$\Pi_{in}(x) = C_1 \left(1 - \frac{1}{(1+Gx)^\alpha}\right), \quad (\text{B.3})$$

where $\alpha = s_0/g$ and $G \equiv Ng$. Eq. (B.3) satisfies the left boundary condition and depends on one constant, C_1 , to be determined below using an asymptotic matching.

2. In the intermediate region, $0 \ll x \ll 1$, the demographic noise is negligible (for any x in this regime, when $N \rightarrow \infty$ the $1/N$ term is much smaller than $gx(1-x)$). Accordingly, the relevant equation is,

$$(gx(1-x))\Pi''_M(x) + (s_0 + g(1-x))\Pi'_M(x) = 0, \quad (\text{B.4})$$

or,

$$\begin{aligned} \Pi''_M(x) + \left(\frac{s_0}{g} \ln' \left(\frac{x}{1-x}\right) + \ln'(x[1-x])\right)\Pi'_M(x) \\ = \left(\Pi'_M \left(\frac{x^{\alpha+1}}{(1-x)^{\alpha-1}}\right)\right)' = 0. \end{aligned} \quad (\text{B.5})$$

This yields,

$$\Pi_M(x) = C_2 \left(\frac{1-x}{x}\right)^\alpha + C_3. \quad (\text{B.6})$$

Here we have two free constants as none of the boundary condition is relevant in the middle regime.

3. Finally, in the outer regime $1-x \ll 1$, x is close to one and $1-2x \approx (-1)$, so we have to consider

$$\begin{aligned} \left(\frac{1}{N} + g(1-x)\right)\Pi''_{out}(x) + (s_0 - g)\Pi'_{out}(x) = 0, \\ \Pi_{out}(1) = 1. \end{aligned} \quad (\text{B.7})$$

obtaining,

$$\Pi_{out}(x) = 1 - C_4(1 - [1 + G(1-x)]^\alpha). \quad (\text{B.8})$$

In fact, the expression (B.9) may be obtained directly from (B.3) using the symmetry of the problem: the chance of a species of abundance x and selection parameter s_0 to win, is the same as its chance to lose if its abundance is $1-x$ and the selective parameter is reversed,

$$\Pi(s_0, x) = 1 - \Pi(-s_0, 1-x). \quad (\text{B.9})$$

Using equations (B.3), (B.6) and (B.9), we can now find the C constants by matching the solutions in the overlap regimes. Π_{in} must match Π_M when $x \ll 1$ but $Gx \gg 1$, meaning that

$$C_1 - \frac{C_1}{(Gx)^\alpha} = \frac{C_2}{x^\alpha} + C_3, \quad C_1 = C_3, \quad G^\alpha C_2 = -C_1. \quad (\text{B.10})$$

A similar matching of Π_M and Π_{out} when both $1-x \ll 1$ and $G(1-x) \gg 1$ yields

$$1 - C_4 + C_4[G(1-x)]^\alpha = C_2(1-x)^\alpha + C_3, \quad 1 - C_4 = C_3, \quad G^\alpha C_4 = C_2. \quad (\text{B.11})$$

Accordingly,

$$\begin{aligned} C_1 = C_3 &= \frac{1}{1 - G^{-2\alpha}} \\ C_2 &= \frac{1}{G^{-\alpha} - G^\alpha} \\ C_4 &= \frac{1}{1 - G^{2\alpha}}. \end{aligned} \quad (\text{B.12})$$

In the large N limit,

$$\begin{aligned} \Pi_{in}(x) &\sim \left(\frac{1}{1 - G^{-2\alpha}}\right) \left(1 - \frac{1}{(1+Gx)^\alpha}\right), \\ \Pi_M(x) &\sim \left(\frac{1}{G^{-\alpha} - G^\alpha}\right) \left(\frac{1-x}{x}\right)^\alpha + \frac{1}{1 - G^{-2\alpha}}, \\ \Pi_{out}(x) &\sim 1 - \left(\frac{1}{1 - G^{2\alpha}}\right) (1 - [1 + G(1-x)]^\alpha). \end{aligned} \quad (\text{B.13})$$

The chance of a single mutant ($n=1$, $x=1/N$, $Gx=Ngx=g$) to win is given by,

$$\Pi_{in}(1/N) = \Pi(n=1) \sim \frac{1 - \frac{1}{(1+g)^{s_0/g}}}{1 - (Ng)^{-2s_0/g}}. \quad (\text{B.14})$$

This approximation is very close to the results obtained from the numerical solution of the exact BKE, as demonstrated in Fig. B.5.

Appendix C. Absorption times

The relevant BKE is,

$$\begin{aligned} \left(\frac{1}{N} + gx(1-x)\right)T''_A(x) + (s_0 + g(1-2x))T'_A(x) = -\frac{1}{x(1-x)}, \\ T_A(0) = T_A(1) = 0. \end{aligned} \quad (\text{C.1})$$

In the inner regime $x \ll 1$

$$\left(\frac{1}{N} + gx\right)T''_{A,in}(x) + (s_0 + g)T'_{A,in}(x) = -\frac{1}{x}, \quad T_{A,in}(0) = 0. \quad (\text{C.2})$$

Accordingly

$$\left(T'_{A,in} \left(\frac{1}{N} + gx\right)^{1+\alpha}\right)' = \frac{\left(\frac{1}{N} + gx\right)^\alpha}{x}. \quad (\text{C.3})$$

The solution that satisfies the left boundary condition is,

$$T_{A,in}(x) = \tilde{C}_1 \left(1 - \frac{1}{(1+Gx)^\alpha} \right) - N \int_0^x \frac{dt}{(1+Gt)^{1+\alpha}} \int^t dq \frac{(1+Gq)^\alpha}{q}. \quad (C.4)$$

The inner integral may be written as

$$\int^t dq (1+Gq)^\alpha \frac{d}{dq} \ln(q) = (1+Gt)^\alpha \ln(t) - \alpha G \int^t (1+Gq)^{\alpha-1} \ln(q) dq \quad (C.5)$$

Plugging (C.5) into (C.4) and using integration by parts to simplify, one obtains,

$$-\alpha G \int_0^x \frac{dt}{(1+Gt)^{1+\alpha}} \int^t (1+Gq)^{\alpha-1} \ln(q) dq = \frac{1}{(1+Gx)^\alpha} \int_0^x \frac{\ln(t)}{(1+Gt)^{1-\alpha}} dt - \int_0^x \frac{\ln(t)}{(1+Gt)^\alpha} dt. \quad (C.6)$$

The last term of (C.6) cancels with the middle term of (C.5) when they both plugged in (C.4). Accordingly,

$$T_{A,in}(x) = \tilde{C}_1 \left(1 - \frac{1}{(1+Gx)^\alpha} \right) - \frac{N}{(1+Gx)^\alpha} \int_0^x \frac{\ln(t)}{(1+Gt)^{1-\alpha}} dt. \quad (C.7)$$

The substitution $z = Gt$ yields,

$$\int_0^x \frac{\ln(t)}{(1+Gt)^{1-\alpha}} dt = \int_0^{Gx} \frac{\ln(z) - \ln(G)}{(1+z)^{1-\alpha}} \frac{dz}{G} = -\frac{\ln(G)}{\alpha G} ((1+Gx)^\alpha - 1) + \frac{1}{G} \int_0^{Gx} \frac{\ln(z) dz}{(1+z)^{1-\alpha}}, \quad (C.8)$$

so finally,

$$T_{A,in}(x) = \left(\tilde{C}_1 + \frac{\ln(G)}{s_0} \right) \left(1 - \frac{1}{(1+Gx)^\alpha} \right) - \frac{1}{g(1+Gx)^\alpha} \int_0^{Gx} \frac{\ln(z) dz}{(1+z)^{1-\alpha}}. \quad (C.9)$$

To match $T_{A,in}$ with $T_{A,M}$ one needs its asymptotic behaviour as $Gx \rightarrow \infty$. Expanding (C.9) one finds,

$$T_{A,in}(Gx \rightarrow \infty) \sim \tilde{C}_1 + \frac{g}{s_0^2} - \frac{\ln(x)}{s_0} - \frac{1}{s_0} \frac{H(\alpha) + \pi \cot(\pi\alpha) + \ln(G)}{(Gx)^\alpha} - \frac{\tilde{C}_1}{(Gx)^\alpha}. \quad (C.10)$$

Using the symmetry $T_A(s_0, x) = T_A(-s_0, 1-x)$ one can find easily the relevant asymptotic behavior of T_{out} ,

$$T_{A,out}(G(1-x) \rightarrow \infty) \sim \tilde{C}_4 + \frac{g}{s_0^2} + \frac{\ln(1-x)}{s_0} + \frac{1}{s_0} \frac{H(-\alpha) - \pi \cot(\pi\alpha) + \ln(G)}{(Gx)^\alpha} - \tilde{C}_4 [G(1-x)]^\alpha. \quad (C.11)$$

The expressions (C.10) and (C.11) should match the intermediate solution $T_{A,M}$ in the relevant regimes. $T_{A,M}$ satisfies,

$$gx(1-x)T''_{A,M}(x) + [s_0 + g(1-2x)]T'_{A,M}(x) = -\frac{1}{x(1-x)}, \quad (C.12)$$

and admits a relatively simple solution

$$T_{A,M}(x) = \tilde{C}_3 + \tilde{C}_2 \left(\frac{1-x}{x} \right)^\alpha - \frac{1}{s_0} \ln \left(\frac{x}{1-x} \right). \quad (C.13)$$

Matching in the regime $x \ll 1 \ll Gx$ one finds

$$\tilde{C}_3 = \tilde{C}_1 + \frac{g}{s_0^2}, \quad \tilde{C}_1 + \beta_1 = -G^\alpha \tilde{C}_2, \quad (C.14)$$

where

$$\beta_1 = \frac{1}{s_0} [H(\alpha) + \pi \cot(\pi\alpha) + \ln(G)].$$

Similarly in the regime $1-x \ll 1 \ll G(1-x)$ the matching yields

$$\tilde{C}_3 = \tilde{C}_4 + \frac{g}{s_0^2}, \quad \tilde{C}_4 + \beta_2 = -G^{-\alpha} \tilde{C}_2, \quad (C.15)$$

with

$$\beta_2 = \frac{1}{s_0} [-H(-\alpha) + \pi \cot(\pi\alpha) - \ln(G)].$$

From these algebraic relations one finds,

$$\tilde{C}_1 = -\frac{G^{2\alpha} \beta_2 - \beta_1}{G^{2\alpha} - 1} \quad (C.16)$$

For a single mutant, the time to absorption $T_{A,in}(1/N)$ is obtained by plugging $\tilde{C}_1$ into (C.9) with $x \rightarrow 1/N$,

$$T_{A,in}(1/N) = \left(\frac{\ln(G)}{s_0} - \frac{G^{2s_0/g} \beta_2 - \beta_1}{G^{2s_0/g} - 1} \right) \left(1 - \frac{1}{(1+g)^{s_0/g}} \right) - \frac{1}{g(1+g)^{s_0/g}} \int_0^g \frac{\ln(z) dz}{(1+z)^{1-s_0/g}}. \quad (C.17)$$

The leading behavior of the time to absorption for a single mutant is given by the large N asymptotics of (C.17),

$$T_A(n=1) \sim \frac{2}{s_0} \left(1 - \frac{1}{(1+g)^{s_0/g}} \right) \ln(N). \quad (C.18)$$

Appendix D. Time to fixation T_f

To obtain the time to fixation (Redner, 2001), one should solve a BKE for

$$Q(x) = \Pi(x) T_f(x). \quad (D.1)$$

This BKE takes the form,

$$\left(\frac{1}{N} + gx(1-x) \right) Q''(x) + (s_0 + g(1-2x)) Q'(x) = -\frac{\Pi(x)}{x(1-x)}, \quad Q(0) = Q(1) = 0. \quad (D.2)$$

We would like to solve for Q in the inner, outer and intermediate regime, using the values of Π obtained in Eqs. (B.12)–(B.13) for each of these regimes.

$$\begin{aligned} \left(\frac{1}{N} + gx \right) Q''_{in}(x) + (s_0 + g) Q'_{in}(x) &= -\frac{C_1}{x} + \frac{C_1}{N^\alpha x \left(\frac{1}{N} + gx \right)^\alpha} \\ Q_{in}(0) &= 0, \quad Q'_M(1-x) + [s_0 + g(1-2x)] Q'_M(x) \\ &= -\frac{C_3}{x(1-x)} - \frac{C_2(1-x)^{\alpha-1}}{x^{\alpha+1}} \\ \left(\frac{1}{N} + g(1-x) \right) Q''_{out}(x) + (s_0 - g) Q'_{out}(x) &= -\frac{1-C_4}{1-x} \\ &- \frac{C_4 N^\alpha \left(\frac{1}{N} + g(1-x) \right)^\alpha}{1-x} \quad Q_{out}(1) = 0. \end{aligned} \quad (D.3)$$

Since (D.2) is linear, the solution for $Q(x)$ in each regime contains a homogenous term which is equal to Π up to a constant, a special solution that has the form of T and another special solution that comes from the last terms if (D.3). Denoting the constants of the homogenous solutions by $\bar{C}$, we obtained, for example,

$$Q_{in}(x) = \bar{C}_1 \left(1 - \frac{1}{(1+Gx)^\alpha} \right) - \frac{C_1 N}{(1+Gx)^\alpha} \int_0^x \frac{dt \ln(t)}{(1+Gt)^{1-\alpha}}$$

$$\begin{aligned}
& + C_1 N \int_0^x \frac{dt \ln(t)}{(1+Gt)^{1+\alpha}} \\
Q_M(x) &= \bar{C}_2 \left(\frac{1-x}{x} \right)^\alpha + \bar{C}_3 - \frac{C_3}{s_0} \ln \left(\frac{x}{1-x} \right) + \frac{gC_2}{s_0^2} \left(\frac{1-x}{x} \right)^\alpha \\
& + \frac{C_2}{s_0} \left(\frac{1-x}{x} \right)^\alpha \ln \left(\frac{x}{1-x} \right) \\
Q_{out}(x) &= \bar{C}_4 (1 - [1 + G(1-x)]^\alpha) - \frac{1 - C_4 N}{(1 + G(1-x))^{-\alpha}} \\
& \times \int_0^{1-x} \frac{dt \ln(t)}{(1+Gt)^{1+\alpha}} - C_4 N \int_0^{1-x} \frac{dt \ln(t)}{(1+Gt)^{1-\alpha}}.
\end{aligned}$$

To match these solutions in the overlap regimes, the constant $\bar{C}$ should satisfy,

$$\begin{aligned}
\bar{C}_3 &= \bar{C}_1 + C_1 \frac{g}{s_0^2} + C_1 \beta_2 & \bar{C}_3 &= \bar{C}_4 + (1 - C_4) \frac{g}{s_0^2} - C_4 \beta_1 \\
-G^\alpha \bar{C}_2 &= \bar{C}_1 + C_1 \beta_1 & -G^{-\alpha} \bar{C}_2 &= \bar{C}_4 + (1 - C_4) \beta_2,
\end{aligned} \quad (D.5)$$

which implies

$$\bar{C}_1 = \frac{2\beta_1 G^{-2\alpha} - 2\beta_2 G^{2\alpha}}{(G^{2\alpha} - G^{-2\alpha})^2}. \quad (D.6)$$

Plugging this into the expression for Q_{in} and evaluating $T_f = Q_{in}/\Pi_{in}$ at $x = 1/N$, one finds the fixation time of a singleton:

$$\begin{aligned}
T_f(1/N) &= T_f(n=1) \sim 2 \left(\frac{[1 + G^{2\alpha}] \ln(G)}{s_0 [G^{2\alpha} - 1]} - \frac{\pi \cot(\pi\alpha)}{s_0} \right. \\
& \left. + \frac{H(\alpha) + G^{2\alpha} H(-\alpha)}{s_0 [G^{2\alpha} - 1]} \right). \quad (D.7)
\end{aligned}$$

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