Environmental stochasticity and the speed of evolution

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Biological populations are subject to two types of noise: demographic stochasticity due to fluctuations in the reproductive success of individuals, and environmental variations that affect coherently the relative fitness of all individuals in the same clone. The rate in which the average fitness of a population increases has been considered so far using models with pure demographic stochasticity; here we present some theoretical considerations and numerical results for the general case where environmental variations are taken into account. Our results suggest that the main effect of environmental stochasticity on the speed of evolution comes from its affect on the chance of a new beneficial mutant to establish. When the dynamics supports a noise-induced stabilizing mechanism, known as the storage effect, mutant establishment is easier and the speed rises when the amplitude of environmental fluctuations increases. For dynamics without this storage effect the effective mutation rate reduces, and the pace of evolution slows down, when the fluctuations grow. We provide analytic solutions for the chance of establishment in a two-species scenario, and compare these predictions with numerical simulations of evolutionary dynamics both in the successional-fixation phase and in the clonal interference phase.

I. INTRODUCTION

Life forms evolve via a continuous process of competition and selection. Malthusian dynamics drives any population to its abundance limit, set by the carrying capacity of its environment and interaction with other populations. In this state the process becomes a zero-sum game and the relative fitnesses of individuals govern their chance to stay alive and reproduce. When the fitness is an inherited feature, like in the case where it reflects the characteristics of a genotype, a new strain (species, haplotype) appears each time a significant mutation happens. The population of strains with beneficial mutations and higher fitness grows, on average, at the account of inferior strains. If the supply of beneficial mutations is unlimited, this process leads to a continuous increase in the average fitness of the whole community.

The rate in which the average fitness increases has been considered by many authors \[1^{\text{-}4}\]. It was shown that the mean fitness growth linearly in time, and the dependence of its speed on the problem parameters, like the community size \(N\), the rate of mutation \(\nu\) and the average strength of a single mutation \(\Delta s\), was analyzed. However, in all these studies the absolute fitness of an individual (and its non-mutant ancestry) is considered to be a time-independent feature. The aim of this paper is to study the case where this assumption is broken, and in particular to consider the effect of environmental stochasticity.

For the sake of concreteness, let us envisage a community of size \(N\) composed of many strains/species of abundances \(n_1, n_2\) and so on (\(\sum n_i = N\)). These species are playing a zero-sum game. Competition takes place by choosing one individual to die and recruiting an offspring of another individual in its place, where the relative fitnesses of the players govern the probabilities of these two choices. The randomness involved in such a process is known as demographic stochasticity and is attributed (like shot noise) to the fact that individuals are discrete. If two species have the same abundance \(n\) and the same fitness, after one generation (i.e., after \(N\) elementary competition events) their abundances will differ, typically, by \(O(\sqrt{n})\).

However, it is hard to imagine a realistic system in which the relative fitness of a certain genotype is actually fixed in time. Environmental variations and changes in the community structure clearly alter the usefulness and effectiveness of different traits, so the effective fitness of a species must fluctuate in time. For example one may consider a case where the time-average of the (logarithmic) fitness of a species is \(s_0\), but the instantaneous fitness will be \(s(t) = s_0 + \eta(t)\), where the (zero mean) function \(\eta\) reflects the effect of the fluctuating environment \[5^{\text{-}7}\].

Here we would like to consider the case where the fitness of a given species reflects the effect of many traits, and the contribution of each of these traits is subject to random environmental variations. Accordingly, \(\eta(t)\) is taken to be an iid random variable chosen independently for each species. These environmentally induced fitness fluctuations are characterized by their strength \(\gamma\) and by the persistence time of the environment, \(\delta\). If the persistence time is, say, one generation (we measure \(\delta\) in units of generations, so in this case \(\delta = 1\)), the abundance of two species that have the same time-averaged fitness \(s_0\) and the same initial abundance \(n\) will differ, after one generation, by \(\gamma n\), so environmental stochasticity is much stronger than demographic noise when the populations are large \[8\].

Many empirical studies show that environmental stochasticity, and the \(O(n)\) fluctuations associated with it, are the general rule rather than the exception \[9^{\text{-}12}\]. As noted by \[6\], all ecological systems are, to a varying extent, subject to stochastic variations in environmental conditions. In fact, we are not familiar with any empirical or even
experimental system where the abundance variations of species or clones were found to be $O(\sqrt{n})$. In particular we would like to refer to the study of Hextra and Leibler [13], where a simple three species microbial community was monitored for three years under strictly fixed environmental conditions (fixed temperature, fixed supply of light which is the only needed resource etc.). Yet, the abundance variation statistics shows $O(n)$ behaviour in most cases and in all cases the strength of abundance variations was much larger than $O(\sqrt{n})$.

Following our recent works on the effect of environmental stochasticity on community dynamics and stability [14–16], here we would like to study how environmental stochasticity affects the evolutionary process and in particular how, and if, it modifies the speed of evolution. To do that we have to present a well-defined generic model of evolution in the presence of environmental variations.

Before undertaking this, we would like to emphasize a crucial observation of past studies. Naively, one would expect that environmental stochasticity destabilizes the dynamics of a community, making fluctuations larger and driving species to extinction more frequently. However, as pointed out by Chesson and coworkers [17–19], under some circumstances environmental stochasticity acts as a stabilizer, a feature known as the "storage effect". As a result, we have to consider two generic models: one for environmental stochasticity without storage, the other with storage.

In the next section we will describe these two scenarios in some detail and explain the way we incorporate them into a model of evolutionary dynamics. In section III we review shortly the problem of the speed of evolution in a system with pure demographic noise, which is our frame of reference. In section IV the chance of establishment of a beneficial mutant, which sets the effective mutation rate, is calculated in the presence of environmental stochasticity with and without storage. The problem without storage has been discussed recently by Cvijović et al [7], and in Appendix B we clarify the relationships between their results and the outcomes of our analysis. In general, we discovered that the chance of establishment decreases as environmental stochasticity increases when there is no storage, while under dynamics with storage stochasticity facilitates the establishment of a mutant.

The results of section IV are the core of our theoretical analysis and are implemented in the next sections. In agreement with the outcomes for a single mutant, the overall speed of evolution is shown to decrease when the environment fluctuates without storage effect (section V), and to increase in the presence of the storage effect (section VI). In both cases the numerics agrees qualitatively with our analysis, and in some particular scenarios we can even show a quantitative agreement between predictions and the outcome of numerical experiments. The fundamental theorem of natural selection [20, 21] is discussed in this context, and we conclude that its extension to noisy systems is problematic. Finally we provide a discussion of the main outcomes of our work and point out a few future directions.

II. TWO TYPES OF ENVIRONMENTAL STOCHASTICITY AND THE STORAGE EFFECT

Environmental variations may affect the fitness of strains or species via many different mechanisms that have to do with many traits. To capture the essence of the problem, we study here two simple zero-sum games for asexually reproductive individuals, where the fitness determines the chance of reproduction.

We consider a closed system that allows for $N$ individuals. Its instantaneous state is fully characterized by a list of strains populations and their relative fitnesses. If $n_i$ individuals in strain 1 have relative fitness $s_1$ and so on, the instantaneous dynamics depends only on the features of the histogram showing how many individuals have relative fitness between $s$ and $s + ds$. Relative fitness is measured from the mean value of the fitness in the population $\bar{s} = \sum_i s_i n_i$, and the speed of evolution $v_{ev}$ is $d\bar{s}/dt$. Only fitness differences $(s_i - s_j)$ play a role in the instantaneous dynamics.

The shape of the fitness histogram reflects (for fixed $N$) the balance between selection and mutation. Selection constantly drives low-fitness species to extinction and therefore reduces the variation in fitness, while mutation generates more and more new strains and broadens the fitness distribution. In the long run the fitness distribution converges to a stable shape of a soliton [2] that moves at constant speed $v_{ev}$. In theories without environmental stochasticity this speed depends on the width of the soliton: when the width is large a new mutant at the leading edge of the soliton grows faster (since the fitness difference between its fitness and $\bar{s}$ are larger) and hence $v_{ev}$ increases.

Now let us describe the two different ways to implement environmental stochasticity into the game.

- Model A (no storage effect): Every elementary competition event is a duel: two individuals out of $N$ are chosen at random (without replacements) and fight against each other. The loser dies, the winner reproduces, and an offspring of the winner takes over the slot of the loser. The chance of an individual to win a duel depends on its relative fitness with respect to its competitor. If individual 1 belongs to species $i$ and its fitness is $s_i$, while 2 belong to species $j$ with $s_j$, 1 wins with probability $P_1$ that depends on $s_i - s_j$, and the chance of 2 to win is $1 - P_1$. Unless otherwise stated (for technical reasons we have used a slightly different form in some of our simulations as explained in Appendix A).
\documentclass[12pt]{amsart}
\usepackage{amsmath,amssymb,amsfonts}
\begin{document}
\begin{equation}
P_i = \frac{1}{2} + \frac{s_i - s_j}{4}.
\end{equation}

- Model B (with storage effect): In this model every competition event involves all the individuals in the community. First, one individual is chosen at random (independent of its fitness) to die. It is then replaced by an offspring that may belong to another species, and the chance of species \( i \) to win the empty slot, \( P_i \), is determined by

\[ P(i) = \frac{n_i e^{s_i}}{\sum_j n_j e^{s_j}}. \]

Model B may describe the dynamics of, say, a forest: individuals are adult trees and the seed bank in the soil reflects the global abundance of each species if seeds from each tree are dispersed at random all over the forest. Upon the death of an adult tree one of the local seeds is chosen to capture the gap with a chance proportional to its fitness, so the overall chance of a species to increase its population reflects both its abundance and its instantaneous fitness, superimposed nonlinearly.

In the "neutral" limit, i.e., when there are no fitness differences between individuals, both models coincide (the chances of a species with abundance \( n_i \) to grow by one or to shrink by one after an elementary competition step are the same). However, when fitness varies in time, the two models differ strongly \[15, 16, 22\]. For a two-species competition under model A, for example, the time to absorption (the time until one of the species goes extinct and the other same). However, when fitness varies in time, the two models differ strongly \[15, 16, 22\]. For a two-species competition under model A, for example, the time to absorption (the time until one of the species goes extinct and the other captures the whole system) scales, as \( N \to \infty \), like \( \ln N/(\Delta s) \), where \( \Delta s \) is the (time independent component of the) fitness difference between the two species. On the other hand under the dynamics of model B the time to absorption scales like \( N^{(1-\tilde{s})/\delta} \), where \( \tilde{s} = 2\Delta s/\gamma^2 \) is the effective strength of selection in this system \[15\]. As long as \( \tilde{s} < 1 \), model B is much more stable than model A because of the storage effect that provides noise-induced stabilization.

To get some intuition for the mechanism that allows the stochasticity to act as a stabilizing factor in model B, let us think about a "winner takes all" version of this model, where the species with higher fitness wins the empty slot for certainty, independent of its abundance. Starting the game with 8 red individuals and 2 green in a community of 10, one elementary competition step is played. When the environment gives higher fitness to the greens, the chance to end up with 7 red and three green is 0.8 (this is the chance that a red is killed), but if the environment is beneficial to the reds their chance to grow is just 0.2. Accordingly, if the environment is neutral on average (i.e., red fitness is higher with probability 1/2) one round ends with 7:3 with probability 0.4 and with 9:1 with probability 1/10. Rare species have a larger chance to grow in abundance just because they are rare, and this implies that the noise acts to stabilize the 50:50 state and to facilitate the invasion of rare species. For a system with many species, in the stable state each of the \( S \) species has abundance \( 1/S \). This effect survives even if one of the species has some average fitness advantage, as shown in \[15, 18\].

On the other hand, if the dynamics of the system takes place in a series of duels, as in model A, the chance for an interspecific duel will be 32/90, and so the probabilities to end up at 9:1 or at 7:3 will be the same: 16/90, meaning that there is no preference for rare or common species and no storage effect.

Another fundamental difference between model A and model B appears when the persistence time of the environment vanishes, \( \delta \to 0 \). Model A reduces, in such a case, to a model with pure demographic noise since one picks the relative fitness independently for each elementary duel. On the other hand, in model B the storage effect is maximal when \( \delta \to 0 \), since, as we have seen, the effect occurs on the level of an elementary event. When \( \delta \) is large, on the other hand, the storage effect disappears \[17\].

Our main goal in what follows is to explain the effect of stochasticity on the evolutionary dynamics with and without storage. To frame our discussion we will start with the simpler case of evolution under pure demographic noise.

### III. PURE DEMOGRAPHIC NOISE

In this section we review shortly some already known results for the speed of evolution in a system with pure demographic noise. To set up the framework for our discussion in the next sections we will try to emphasize two basic aspects of the analysis, namely the chance of establishment of a beneficial mutation and Fisher’s fundamental theorem of natural selection.

We consider a system of \( N \) individuals playing a zero sum game, where the average number of offspring per individual depend on its fitness \( s \). For the sake of concreteness let us consider a series of duels (as explained above, without environmental noise, model A and model B coincide). In each elementary time-step two individuals are chosen at
| Term        | Description                                                                                                                                                                                                 |
|-------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| $N$         | number of individuals in the community.                                                                                                                                                                 |
| $n_i$       | number of individuals belonging to species $i$.                                                                                                                                                         |
| $x_i$       | population fraction of species $i$, $x_i = n_i/N$.                                                                                                                                                      |
| $\delta$   | correlation time of the environment, measured in generations. The time between environmental shifts is taken from an exponential distribution with mean $\delta$.                                               |
| $\Pi_{n=1}$| The chance of a single mutant to establish (for model A and pure demographic noise we used the chance of fixation instead, since the differences between establishment and fixation are minor. |

$s$ the relative (logarithmic) fitness of a species. $s = s_0 \pm \eta(t)$.  
$s_0$ the time-independent component of the fitness.  
$\gamma$ the amplitude fitness fluctuations.  
g $\equiv \delta \gamma^2 / 2$ scaled environmental stochasticity.  
$\delta s / \gamma^2$ scaled selection (mainly relevant to model B).  
$\nu$ mutation rate.  
$\Delta s$ average strength of a single mutation  
$\bar{s}/s_0$ the average instantaneous/time independent fitness  
v$_{ev}$ speed of evolution, $d\bar{s}/dt$.

random and an offspring of the winner replaces the loser, the chance of individual $i$ to win against $j$ is $1/2+(s_i-s_j)/4$. With probability $\nu$ the offspring mutate, and its fitness is the fitness of its parent plus or minus a fixed number $\Delta s$.

First we discuss a system with $N-1$ individuals with the same fitness $s$ and one beneficial mutant with $s = s_0 + \Delta s$, assuming (as in the rest of this paper) that selection is strong in comparison with demographic noise, i.e., $N \Delta s \gg 1$. In a two species game of this kind the lineage of this mutant will go extinct with probability $1 - \Delta s$ and will take over the system with probability $\Delta s$ (see next section for detailed calculations). Accordingly, the average number of generations between two successful mutations is

$$\tau_1 = \frac{2}{\nu N \Delta s}.$$  

The time to fixation of a beneficial mutation is known to be [23],

$$\tau_2 = \frac{\ln(N)}{\Delta s}.$$  

If $\tau_1 \gg \tau_2$ (meaning that $\nu \ll 2/[N \ln(N)]$), the system is in its successional-fixation (one locus) regime: from time to time a beneficial mutation appears and takes over the community, leading to an increase of the average fitness by $\Delta s$. $\bar{s}$ grows in steps, each corresponds to a single fixation of a successful beneficial mutation. The average velocity of evolution is

$$v_{ev} = \frac{\Delta s}{\tau_1 + \tau_2} = \frac{\nu N (\Delta s)^2 / 2}{1 + \frac{\nu N \ln(N)}{2}}.$$  

This behavior is demonstrated in Figure [1].

When $N$ (or $\nu$) increases the system leaves the successional-fixation regime and enters the clonal interference regime [24], where many clones with different fitness levels compete and mutate at the same time. Unlike [4], here we make no distinction between ”clonal interference” and ”multiple mutations” as two different approximate pictures of the evolutionary dynamics in the multiple species phase, so our clonal interference regime is everywhere outside the successional-fixation region of parameters.

In this phase the growth of $\bar{s}$ is continuous, not stepwise, since new beneficial mutations appear (and the abundance of their lineage grow) in parallel. In this phase, as we mentioned above, the steady state is a soliton that moves in a constant velocity. Since the growth rate of the most beneficial clone (at the leading edge of the soliton) is determined by its fitness advantage with respect to the average individual, it is clear that the width of the soliton sets the velocity...
FIG. 1: The increase in the average fitness of a community, $\bar{s}$, as a function of time (measured in generations). Results are shown for a community of $N = 10^5$ individuals, simulated with $\nu = 10^{-5}$, where $\Delta s = 0.08$, 0.16 and 0.25 (green, yellow and red lines, correspondingly). The dashed black lines are the predictions of (4) in each case. The pronounced steps in $\bar{s}$ show that the system is indeed in its successional-fixation phase.

FIG. 2: The increase in the average fitness of a community, $\bar{s}$, as a function of time (main panel). Results are shown for a community of $N = 10^5$ individuals, simulated with $\nu = 0.1$ and $\Delta s = 0.01$, in the clonal interference phase. A histogram (upper left) shows the number of individuals at each fitness level at the endpoint of the simulation ($t = 10000$). Fisher’s fundamental theorem of natural selection is demonstrated in the lower-right inset, where the fitness variance (red) and $v_{ev}$ (local derivative of $\bar{s}(t)$, smoothed over 20 points) are plotted together.

of evolution. In fact, Fisher’s fundamental theorem of natural selection [20, 25] states that the instantaneous speed of evolution is equal to the instantaneous genetic variance in fitness. Figure 2 demonstrates these aspects of the theory using our simulations.

To summarize, the main factor that governs the growth rate of the fitness is the chance of establishment of a beneficial mutation, which is translated into the timescale $\tau_1$, where the time it takes for a beneficial mutation to capture the system $\tau_2$ provides relatively small corrections. In the successional-fixation phase these numbers govern the speed of evolution (Eq. 4 and Fig. 1). In the clonal interference phase the situation is more complicated, but the fundamental theorem of natural selection allows one to relate the speed of evolution to the width of the moving soliton. In the next section we will calculate the chance of establishment in the presence of environmental stochasticity for both model A dynamics (without storage effect) and model B (with storage): this will provide us a basic intuitive argument that explains qualitatively, and sometimes even quantitatively, the numerical results that we present later on.
IV. THE CHANCE OF ESTABLISHMENT OF A BENEFICIAL MUTATION

Let us consider a population of size $N$ where all the individuals have the same fitness, except of the single mutant that has higher fitness (for the moment we neglect the possibility of subsequent mutations). On average the mutant population grows exponentially, so in the absence of stochasticity the mutant lineage will take over the system with probability one. However, if the probability of the mutant to win a duel is, say, 0.51, there is a decent chance that its lineage will reach extinction during the first rounds of competition. Only when the mutant lineage reaches some critical abundance $n_c$ the noise is averaged out and its population starts to prosper reliably. In this section we would like to calculate the chance of a single beneficial mutant to establish. For pure demographic noise and for model A this quantity is almost equal to the chance of fixation; for model B the situation is slightly more complicated as we will explain below.

Technically, the chance of a species of abundance $n$ to reach fixation, $\Pi_n$, is related to $\Pi_{n\pm1}$ via the (homogenous version of the) Backward Kolomogorov equation (BKE) [26],

$$\Pi_n = T_{n\to n+1}\Pi_{n+1} + T_{n\to n-1}\Pi_{n-1} + T_{n\to n}\Pi_n,$$  \hspace{1cm} (5)

where $T_{n\to n\pm1}$ is the chance for an increase or decrease of the population by a single individual given $n$ and the boundary conditions are $\Pi_0 = 0$ and $\Pi_N = 1$.

A. Pure demographic noise

For a system with pure demographic noise and selection (here we denote $s_0$ the difference in the log fitness between the two species) we assume,

$$T_{n\to n\pm1} = \left(\frac{1}{2} \pm \frac{s_0}{4}\right) \left(\frac{2n(N-n)}{N^2}\right).$$

In the continuum limit we define $x = n/N$ and Eq. (5) takes the form,

$$\frac{1}{2N}\Pi''(x) + \frac{s_0}{2}\Pi'(x) = 0.$$  \hspace{1cm} (6)

The solution [27], subject to to boundary conditions $\Pi(0) = 0 \quad \Pi(1) = 1$, is given by (we have translated back $x$ to $n/N$),

$$\Pi(n) = \frac{1 - e^{-s_0n}}{1 - e^{-s_0N}}.$$  \hspace{1cm} (7)

In the large $N$ limit the chance of a single beneficial mutant to reach fixation is $\Pi_{n=1} = 1 - e^{-s_0} \approx s_0$. Another way to get the same result is to conclude from (7) that the chance of fixation becomes significant at $n_c = 1/s_0$; above this point the growth is more or less deterministic while below this point the deterministic effects are negligible, again one finds that the chance of fixation is actually the probability of reaching $n = 1/s_0$ under neutral dynamics, yielding again

$$\Pi_{n=1}^{Dem} = s_0.$$  \hspace{1cm} (8)

B. Model A: Environmental stochasticity without storage

Here we would like to find the equivalent of (7) for a system under environmental stochasticity without storage (model A). To do that, we are using the telegraphic noise system that was presented and analyzed in [15, 22] for a two species system of $N$ individuals. In this model the environment is kept fixed for a certain time $\tau$, and then it shifts randomly to another state. $\tau$ is taken from an exponential distribution with mean $\delta$, so the chance of environmental shift between two elementary competition events is $1/(N\delta)$. Some aspects of model A dynamics were considered recently by Cvijović et al [7], and we will comment below (in particular, in Appendix B) about the similarities and differences between our results.

For model A, as explained above, in each elementary timestep two individuals are chosen at random for a duel and an offspring of the winer replaces the loser where the chance to win the competition is determined by the relative
fitness. In fluctuating environment we should distinguish between $s_0$, the time independent component of the fitness, and $s(t)$, the instantaneous fitness. Therefore, the chance of an individual to win a competition is,

$$1/2 + \eta(t)/4 + s_0/4,$$  \hspace{1cm} \text{(9)}

and the chance of losing the duel is $1/2 - \eta(t)/4 + s_0/4$ (here $s_0$ is the difference in the average fitness between the two individuals $i$ and $j$, $s_0^i - s_0^j$, and $\eta$ is defined similarly). When $\eta(t) = 0$, the dynamics reduces to the pure demographic noise case considered above.

In our telegraphic model after an average number of $\delta N$ elementary time-steps $\eta(t)$ is chosen randomly (and independently for each species) to be either $\gamma$ or $-\gamma$, so the system is characterized by a time independent selective advantage $s_0$ superimposed on fitness variations of amplitude $\gamma$ and correlation time (measured in units of a generation time) $\delta$. Thinking about abundance variations in stochastic environment as a random walk in the logarithmic abundance space (as the population grows or decays exponentially during good/bad periods) one may identify the quantity

$$g = \gamma^2 \delta/2$$

as the ”diffusion constant” associated with the environmental fluctuations [28].

This model, although simple, present a difficult mathematical problem since the relevant BKE involves two coupled, second order equations. Fortunately, in [15] we have identified the effective BKE for the large $N$ limit of this dynamics and studied it in the context of the time to absorption (fixation/extinction) problem. For the problem at hand, the relevant form of the BKE may be taken directly from appendix 3 of [15] and is given (we are using the same notations as [15], except for using $s_0$ for the time-independent component of the selection instead of $\eta_0$) by,

$$\left(\frac{1}{N} + gx(1-x)\right)\Pi''(x) + (s_0 + g(1-2x))\Pi'(x) = 0.$$  \hspace{1cm} \text{(10)}

Equation (10) may be solved by direct integration, but we find it more instructive to analyze it using boundary layer theory. Since the effect of demographic stochasticity appears only in the $1/N$ term, we can consider two overlapping regimes in the range $0 \leq x \leq 1$: the inner region $x \ll 1$ where $1 - x \approx 1$ and the outer region, $gNx \gg 1$, where the $1/N$ term is negligible. Solving in each region separately, plugging the boundary conditions and matching the two solutions to determine the remaining constants of integration one finds:

$$\Pi_{in}(x) = 1 - \frac{1}{(1 + gNx)^{s_0/g}}$$

$$\Pi_{out}(x) = 1 - \left(\frac{1-x}{gNx}\right)^{s_0/g},$$

so the uniform approximation is

$$\Pi_{uni}(x) = 1 - \left(\frac{1-x}{gNx}\right)^{s_0/g} - \frac{1}{(1 + gNx)^{s_0/g}} + \frac{1}{(gNx)^{s_0/g}}.$$  \hspace{1cm} \text{(12)}

Figure [5] demonstrates the accuracy of these approximation even for relatively small values of $N$.

As $N \to \infty$, the crossover to the deterministic dynamics takes place in the inner regime, so the critical value of $n$ (note that $Nx = n$) is at

$$n_c = \frac{e^{g/s_0} - 1}{g}.$$  \hspace{1cm} \text{(13)}

This result converges to the limit $n_c = 1/s$ when the environmental stochasticity vanishes ($\gamma = g = 0/ s = s_0$), but it implies that when $g \gg s_0$, $n_c$ grows exponentially with $g$, meaning that it is much harder for a more beneficial mutant to invade. For $n_c$ to be above some threshold value $n = Nx_1$ one needs, in the limit $g \gg s_0$, $s_0 < g/\ln(gNx_1)$. This formula is equivalent to Eq. [9] of [7], see Appendix B for a detailed discussion.

A similar expression, more relevant to our purposes, is the chance of a single individual with a beneficial mutation to take over the system,

$$\Pi_{n=1}^{\text{Model A}} = 1 - \frac{1}{(1 + g)^{s_0/g}}.$$  \hspace{1cm} \text{(14)}

In conclusion, under model A dynamics, when the strength of the environmental stochasticity increases:
The chance of establishment decreases

• The region of parameters that corresponds to the successional-fixation phase widens.

These conclusions, on their face, contradict the claims of [7], stating that environmental variation increase the chance of successful invasion. In Appendix B we show that, for finite N, there is a regime where indeed environmental variation assists invasion, but this regime disappears in the large N limit.

C. Model B: Environmental stochasticity with storage

Now let us consider model B dynamics, where the storage effect acts to stabilize the coexistence state. Under storage and without selective advantage, the average lifetime of a two-species system (starting, say, from the point of maximum lifetime which, by symmetry, is at \(x^* = 1/2\)) scales like \(N^{1/\delta}\) if \(\delta < 1\) [15 22]. In the presence of selection the symmetry between species is broken and \(x^*\) is not at 1/2, yet the time to absorption scales like \(N^{(1-\hat{s})/\hat{s}}\), where \(\hat{s} = 2s/\gamma\). This means that the system is relatively stable as long as \(\hat{s} < 1\), i.e., when the environmental noise amplitude is large with respect to the strength of selection.

When discussing the evolutionary game and the establishment of a favored mutation, the relevant quantity is the chance of a mutant’s lineage to reach some threshold density where the chance of stochasticity induced extinction event is small. For the cases considered above, i.e., purely demographic system and a system with environmental noise but without storage, the relevant quantity is \(\Pi_{n=1}\), the chance of the mutant to capture the whole system, since after crossing the dangerous zone where fluctuations are important a beneficial species grows exponentially and takes over the whole community in logarithmic time. This is not the case when storage effect stabilizes a fixed point at \(x^*\): here the relevant quantity is the chance to reach \(x^*\) or, (since it is difficult to find \(x^*\)) some other threshold level as, for example, \(x = 1/2\). Accordingly, we would like to import the homogenous BKE from [15] and to solve it with the boundary conditions \(\Pi(0) = 0\) and \(\Pi(q) = 1\). We are not going to determine the exact value of \(q\), but one may think about it as a number close to 1/2.

The relevant equation is (see [15], section VI) is,

\[
\left(\frac{1}{N} + gx(1-x)\right)\Pi''(x) + \left[s_0 + g(1-2x)\left(1 + \frac{1}{\delta}\right)\right]\Pi'(x) = 0.
\] (15)

Note that Eq. (10) is the limit of (15) when \(\delta \to \infty\).

The inner solution of (15), in the region \(x \ll 1\), is relatively simple,

\[
\Pi^{in}(x) = C_1\left(1 - \frac{1}{(1 + gNx)^{\frac{s_0 - 1}{\gamma + 1}}}\right).
\] (16)

Again, since the region affected by stochasticity is always inside the inner regime when \(N \to \infty\), the only important factor that is left to be determined is the value of \(C_1\) that has to match the outer solution.
In the outer regime the $1/N$ term is negligible and (15) may be written as

$$\Pi''(x) + \left[\frac{s_0}{g} \ln'(\frac{x}{1-x}) + \left(1 + \frac{1}{\delta} \right) \ln'(x(1-x))\right]\Pi'(x) = 0.$$  

Using integration factor one finds the solution that satisfies $\Pi(q) = 1$,

$$\Pi_{\text{out}}(x) = 1 - C_2 \int_x^q dt \frac{(1-t)\frac{s_0}{g} t^{-1-\frac{1}{\delta}}}{t^{\frac{2\alpha}{g} + \frac{1}{\delta}}}.$$  

(17)

To match the inner and the outer solutions one would like to compare $\Pi_{\text{out}}$ at $x \ll 1$ with $\Pi_{\text{in}}$ at $gNx \gg 1$. Clearly,

$$\Pi_{\text{in}}(gNx \gg 1) \sim C_1 - \frac{C_1}{(gNx)^{\frac{\alpha}{g} + \frac{1}{\delta}}},$$  

(18)

and a more cumbersome analysis yields,

$$\Pi_{\text{out}}(x \ll 1) \sim 1 - C_2 A - \frac{C_2}{\left(\frac{s_0}{g} + \frac{1}{\delta}\right)x^{\left(\frac{2\alpha}{g} + \frac{1}{\delta}\right)}},$$  

(19)

with $(\delta \equiv 2s_0/\delta)$

$$A \equiv -2 F_1\left(1 + \frac{\delta+1}{\delta}, \frac{\delta+1}{\delta}, 1 - \frac{\delta+1}{\delta}, q\right).$$

Matching (16) with (19) one finds,

$$C_1 = 1 - \frac{\alpha A}{(gN)^{\alpha} + \alpha A}, \quad C_2 = \frac{\alpha}{(gN)^{\alpha} + \alpha A},$$  

(20)

where $\alpha \equiv (s_0/g) + (1/\delta)$. Since $A$ is a finite number that does not scale with $N$, as $N \rightarrow \infty$ one obtains $C_1 \rightarrow 1$, independent of the choice of $q$ as long as $q < 1$.

Given the above, the chance of establishment of a beneficial mutation at large $N$, i.e., the Model B equivalent of Eq. (14), is

$$\Pi_{\text{Model B}}_{\text{Model B}} = 1 - \frac{1}{(1+g)^{\frac{2\alpha}{g} + \frac{1}{\delta}}}.$$  

(21)

As oppose to model A, $\Pi_{\text{Model B}}_{\text{Model B}}$ grows with $g$. Thus, in systems which are subject to storage, as the strength of the environmental stochasticity increases:

- The chance of establishment increases.
- The region of parameters that corresponds to the successional-fixation phase becomes narrower.

Once we calculated the chance of establishment, Eqs. (14) and (21), we can proceed to consider the evolutionary dynamics of many species.

V. SPEED OF EVOLUTION IN MODEL A: ENVIRONMENTAL NOISE WITHOUT STORAGE

In section III above we argued for a general expression for the speed of evolution in the successional-fixation phase, $\nu_{ev} = \Delta s/(\tau_1 + \tau_2)$, where $\tau_1$ is determined by the chance of establishment of a beneficial mutation. Given the results of the last section and in particular Eq. (14), one expects that in the presence of environmental stochasticity with no storage effect,

$$\tau_1^{\text{Model A}} = \frac{2}{\nu N \Pi_{\text{Model A}}} \frac{2}{\nu N \left(1 - \frac{1}{(1+g)^{\alpha/\delta}}\right)}.$$  

(22)
FIG. 4: $\bar{s}_0$ vs. time in the successional-fixation phase of model A, with environmental stochasticity and without storage. Results are shown for $N = 10^5$, $\gamma = \sqrt{2}$, $\delta = 3$, with $\Delta s = 0.25$ (left panel) and $\Delta s = 0.5$ (right panel). Each run yields a single curve and one can see the pronounced stepwise structure. The average (thick red line) is very close to the prediction of (23) (thick blue curve) and differs substantially from the demographic noise prediction (4) (thick black line). In the left panel the average was taken from 10 runs. In the right panel the average was taken from 100 runs, only a few of them are shown.

In the large $N$ limit, $\Pi_{n=1}^{\text{Dem}} = 1 - \exp(-s_0)$, while $\Pi_{n=1}^{\text{Model A}} = 1 - \exp(-s_0 \ln(1 + g)/g)$. Since $\ln(1 + g)/g$ is a monotonously decreasing function for $g \geq 0$, the chance of establishment under environmental noise (for the same $s_0$) is always smaller than the chance of establishment with pure demographic stochasticity. This provides us the basic intuitive argument, namely, that the speed of evolution slows down under environmental stochasticity without storage.

Let us present now a few numerical results. Our numerical procedures are outlined in Appendix A.

It is not easy to probe the successional-fixation phase using our numerics. The difference between $\Pi_{n=1}^{\text{Dem}}$ and $\Pi_{n=1}^{\text{Model A}}$ is determined by $\ln(1 + g)/g$, so to get a factor of $1/4$, say, one needs $g \equiv \gamma^2 \delta / 2 \approx 10$. On the other hand Eq. (9) implies that $\gamma$ must be smaller than $2 - \Delta s$. If the value of $\delta$ increases to 10 generations, say, the system enters the regime where fixation occurs in a single sweep and there is no random walk in the log-space, so our choice of parameters is quite constrained.

Taking $\delta = 3$ and $\gamma = \sqrt{2}$, we were able to compare our prediction,

$$v_{ev}(\gamma) = \frac{\nu N (\Delta s) \Pi_{n=1}^{\text{Model A}} / 2}{1 + \nu N \ln(N) \Pi_{n=1}^{\text{Model A}} / (\Delta s)},$$

(23)

with the numerics in the regime where the outcome of (23) differs substantially from the demographic noise prediction (4). The results are shown in Figure 4. The agreement between (23) and the outcome of the simulation is evident, as well as the disagreement between the numerics and (4). Moreover, one can see that the stochasticity actually slows down the speed of evolution, as expected.

In the clonal interference phase we have no analytic predictions and the main numerical results are illustrated in Figures 5, 6, and 7. The mean fitness of the whole community still grows linearly in time, but the speed of evolution decreases monotonically as $\gamma$ increases. For fixed $\gamma$, the relative effect of the environmental noise, $v_{ev}(\gamma)/v_{ev}(\gamma = 0)$, decreases as $N$ grows, as shown in Figure 6, but the rate of decrease slows down considerably with $N$. Although the relative effect becomes smaller as $N$ increases, it is still pronounced. Since the speed of evolution diverges as $N \to \infty$ it is difficult to speak about the effect of environmental noise in the asymptotic limit.

Finally, it appears as if Fisher’s fundamental theorem of natural selection breaks down under environmental stochasticity. This statement is, in some sense, trivial: as seen clearly in Fig. 4 while the variance is always positive, environmental variations may cause the mean of $s_0$ to decrease, since at a certain period the environment may favor a species with low $s_0$ for an arbitrary long time [21]. Still one may suggest that the fundamental theorem may hold on average, when $\text{var}(s_0)$ and the average speed are compared.

In practice, this is not the case. While at each moment the rate of growth of the instantaneous fitness of the community, $ds/dt$, is equal to the instantaneous variance of $s$, the same statement is not true with regard to $s_0$. As demonstrated in Figure 7 as $\gamma$ grows the variance of $s_0$ (when averaged over long periods of time) increases while the values of $d\bar{s}_0/dt$ decrease.
FIG. 5: The increase in the average fitness of a community as a function of time. Results are shown here for a community of $N = 10^4$ individuals, simulated with $\delta = 0.1$, $\nu = 0.01$ and $\delta s = 0.01$. The lines show the average fitness $\bar{S}$ as a function of time, where time is measured in generations. The speed of evolution is highest when $\gamma = 0$ (blue line) and decreases as $\gamma$ grows.

FIG. 6: The speed of evolution (the slope measured from curves like those presented in Fig. 5) when plotted against $\gamma$ for $N = 1000$ (black full line and circles), $N = 10^4$ (red dashed line and squares) and $N = 10^5$ (blue dotted line and diamonds). All slopes were obtained from simulation of $10^6$ generations, with $\Delta s = 0.01$ and $\nu = 0.01$. The speed of evolution increases with $N$ but for each $N$ it decreases with $\gamma$ (inset). The relative effect, $v_{ev}(\gamma)/v_{ev}(\gamma = 0)$ becomes slightly smaller as $N$ increases (main panel).

VI. SPEED OF EVOLUTION IN MODEL B: ENVIRONMENTAL NOISE WITH STORAGE

While in model A the chance of a beneficial mutant to establish reduces as $\gamma$ increases, the opposite is true when the dynamics allows for the storage effect, as in model B. The effect enhanced the chance of invasion of any rare species, so the establishment rate is higher. Since the establishment rate is the main factor that determines the speed of evolution, we expect that under storage the speed of evolution increases with the strength of environmental stochasticity.

The chance of establishment in general has the form $\Pi_{n=1} = 1 - e^{-x}$, where $x_d = s_0$ for pure demographic stochasticity and $x_s = \ln(1 + g)((s_0/g) + (1/\delta))$ for model B. Since $x_s$ is a monotonously increasing function of $g$ it is always larger than $x_d$. Accordingly, we hypothesize that the speed of evolution is an increasing function of $\gamma$. For small $g$, $x_s \approx s_0 + g/\delta$ while for large $g$, $s_0 \approx \ln g/\delta$, meaning that the rate of increase of $v_{ev}$ with $\gamma$ slows down as $\gamma$ increases.
FIG. 7: The speed of evolution (the slope measured from curves like those presented in Fig. 5, blue squares) and the average variance of $s_0$ (red circles), both plotted against $\gamma$ for for simulations with $N = 10^4$, $\nu = 0.01$, $\delta = 0.1$ and $\Delta s = 0.1$. For each value of $\gamma$ the data were extracted from a run with $10^4$ generations. In the inset one can see the instantaneous values of the variance and the velocity as measured during 1000 generations of the run with $\gamma = 2.6$, where the differences between the two quantities are pronounced.

FIG. 8: $s_0$ vs. time at the successional-fixation phase with and without environmental stochasticity with storage (model B). A single typical history (solid line) and an average over 3000 samples (dashed lines) are shown for $\gamma = 0$ (red) and $\gamma = 1/2$ (blue), with $\delta = 0.2$, $\nu = 10^{-4}$, $N = 100$ and $ds = 0.125$. Clearly the speed of evolution is growing with $\gamma$, as opposed to the behavior without storage (model A) demonstrated in Figure 4.

This is indeed the case. Figure 8 demonstrates the effect of environmental noise in the successional-fixation phase: the average slope increases as the width of the stairs (which is a measure of $\tau_1 + \tau_2$) decreases, since it is easier for new mutant to invade. Because of that we have to take $\nu$ to be much smaller than $1/N \ln N$ in order to be in the successional-fixation phase.

In the clonal interference phase we observed the same behavior. The velocity grows with $\gamma$, first almost linearly and then the graph levels off (Figure 9). In the region of parameters we have checked, our simulations (not shown) also suggest that the relative increase in the velocity becomes larger as $N$ increases, as opposed to the outcome of the same numerical experiment without storage.
FIG. 9: $v_{ev}$ vs. $\gamma$ in the clonal interference phase. For 11 values of $\gamma$, $\overline{s_0}$ was plotted against time for 10000 generations (lower inset) and the measured slope was plotted against the values of $\gamma$ (blue circles). As in the successional-fixation phase, $v_{ev}$ increases with $\gamma$, and as predicted from the expression derived for the probability of establishment, the graph levels off as $\gamma$ grows. In the upper left inset the same $v_{ev}$ points (blue) are shown together with the variance of $s_0$ (red): while $v_{ev}$ grows, the variance grow even faster. The parameters of the simulation were $N = 1000$, $\nu = 0.01$, $\delta = 0.1$ and $\Delta s = 0.2$.

Finally, we observe again that Fisher’s fundamental theorem does not hold for the (time averaged) variance of the time independent component of the fitness $s_0$, since it grows even faster than $v_{ev}$ (inset of Figure 9).

While the qualitative agreement between our prediction and the numerical results is satisfactory, for model B we cannot compare the analytical results and the numerics quantitatively. The simulation procedure for model B is more complicated and the size ($N$) of the communities we can simulate for many generations is quite limited, meaning that the applicability of asymptotic expressions like Eq. (21) is restricted. The successional-fixation phase is extremely narrow when the storage effect dominates the dynamics and it disappears very fast as $N$ increases, while in the clonal interference phase the shape of the soliton, for which we have no theory so far, appears to play a central role.

VII. DISCUSSION

The "speed of evolution" problem belongs to the general field of spatial invasion of a stable state into an unstable one. Not surprisingly, the first to consider this problem was R. A. Fisher [29], who suggested his famous equation,

$$\frac{\partial \rho (x,t)}{\partial t} = D \frac{\partial^2 \rho (x,t)}{\partial x^2} + a[\rho (x,t) - \rho^2 (x,t)],$$

(24)

to describe the spreading of a favored mutation in a spatially structured population. Here $\rho (x,t)$ is the fraction of the local population that have the favored mutation, $a$ is the local growth rate of this fraction (and is proportional to the selective advantage of the mutation) and $D$ is the spatial diffusion constant. Fisher equation is known to support a front that propagates with velocity $2\sqrt{Da}$; this velocity is determined, as in other cases of what is known as "pulled fronts", by its leading edge [30].

In the context of evolution, space is translated to fitness ($x \rightarrow s$), the diffusion constant is the effective mutation rate and $a$, the growth rate of a clone with fitness $s$, is simply $s - \bar{s}$, the distance from the mean. The corresponding equation is,

$$\frac{\partial \rho (s,t)}{\partial t} = \nu_{eff} \frac{\partial^2 \rho (s,t)}{\partial x^2} + \rho (s,t) \int_{-\infty}^{\infty} ds' (s - s') \rho (s',t) = \nu_{eff} \frac{\partial^2 \rho (s,t)}{\partial x^2} + (s - \bar{s})\rho (s,t).$$

(25)

This is a Fisher-like equation with nonlocal competition, but the competition kernel is asymmetric and increases with he distance, unlike the cases that were studied in the literature in this context [31, 32]. Multiplying both sides of Eq. (25) by $s$ and integrating over $s$ one may easily derive the relationship $\dot{\bar{s}} = \overline{s^2} - \bar{s}^2$, i.e., Fisher’s fundamental theorem of natural selection.
It may be very interesting to consider the effect of demographic and environmental stochasticity on the features of (25) by adding terms like $\xi(x,t)\sqrt{\rho}$ (for demographic stochasticity) and $\xi(x,t)\rho$ (for environmental stochasticity), where $\xi$ and $\zeta$ are white noise. The resulting equations may be analyzed perturbatively to reveal the effect of noise in a neatly arranged fashion. Our result suggest that the main effect of these perturbations is the renormalization of the "diffusion constant" $\nu$, which in turn may affect the width of the moving soliton.

In general, we have seen throughout this paper that the effect of stochasticity on the effective mutation rate is the crucial factor that determines the speed of evolution: $v_{\text{exp}}$ grows when $\Pi_n=1$ increases and the soliton slows down when $\Pi_n=1$ decreases. The width of the soliton appears to have a secondary role: the variance of $s_0$ always grows with $g$, but the velocity may decrease.

In the large $N$ limit the response to environmental stochasticity in the absence of the storage effect is opposite to the response in the presence of the storage. This observation may be important for many studies of eco-evolutionary dynamics, like the analysis of long-term microbial evolution [21], empirical assessment of the fitness diversity in a population [10] and even for the ability to predict the chance of a species to survive external stress by rapidly evolving new adaptations [33].

The model considered here is, we believe, generic. Yet, in practice one may expect some deviations from its simplifying assumptions. In natural community that evolves via selection and mutation, the response of different species to the environmental variation is perhaps at least partially correlated, a correlation that decays with the genetic distance. In parallel, the strength of competition between species may decay with the distance to their common ancestor (the competitive-relatedness hypothesis) [34]. A reliable entanglement of these effects in empirical system may become a formidable task, but the basic intuitive argument presented in this work may provide a few simple guidelines for such an analysis.

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Appendix A: Numerical procedure

1. Model A

We have simulated a community of $N$ individuals that may belong to different species, where the fitness of each species or strain is characterized by two numbers: its time-averaged value $s_0$ and its instantaneous value $s$. In the initial state all individuals except one belong to species 1 with average fitness $s_0 = 0$, one individual belongs to species 2 with average fitness $s_0 = \Delta s$.

During each elementary timestep one individual is chosen at random. With probability $\nu$ this is a mutation step and a number $\Delta s$ (with probability $1/2$) or $-\Delta s$ is added to both the average fitness $s_0$ and the instantaneous value $s$.

With probability $1 - \nu$ this is a competition step: another (different) individual is chosen at random to compete with the already chosen one. The chance of an individual $i$ to win the competition against $j$ is

$$P_i = \frac{1}{1 + e^{s_j - s_i}}.$$  

(A1)

An offspring of the winner, that inherits its parent average and instantaneous fitness, then replaces the loser.

Environmental variations are responsible to the difference between $s_0$ and $s$, and are characterized by the strength of variations $\gamma$ and the correlation time of the environment $\delta$. After each elementary timestep the environment flips with probability $1/(N\delta)$. After each shift of this type the instantaneous fitness of each species $n$ is set to be $s^n = s_0^n + \eta^n$, where $s_0$ is the same number as before and $\eta$ is picked, independently for any species, from a uniform distribution with width $\sqrt{12\gamma}$.

Note that Eq. (A1) differs from the winning probability (9) used in our theoretical calculations. We have to use (A1) because in the clonal interference phase the values of $s_j - s_i$ are not limited, while $P_i$ should be between zero and one. Clearly, up to a factor of two (9) is the weak selection limit of (A1). In practice we have used (A1) in the clonal interference phase and (9), with $\eta = \pm \gamma$, in the successional fixation phase where we are trying to compare our results with the theoretical formulas.

2. Model B

The only difference between the simulations of model A and model B occurs during the elementary competition step.

In model B one individual, $i$, is chosen at random. With probability $\nu$ it mutates (using the same procedure as above) and with probability $1 - \nu$ it dies. Upon death, another individual $j$ is chosen to replace $i$. The probability that $j$ belongs to species $k$ is given by,

$$P_k = \frac{\eta_k e^{s_k}}{\sum_l \eta_l e^{s_l}}.$$  

(A2)

To facilitate the numerics we have implemented a slightly different version of (A2). Upon the death of $i$ another individual $j \neq i$ is chosen at random, and is rejected (to reproduce and fill the empty slot with its offspring) with probability $1 - \exp(s_j - s_{max})$, where $s_{max}$ is the maximum instantaneous fitness, so if this individual fitness is $s_{max}$ it is accepted for certainty. Upon rejection, another individual is picked at random and the procedure is iterated until the first acceptation. Using this method the chance of a species to increase its abundance depends both on its abundance (that affects the chance of $j$ to belong to this species) and its fitness (that dominated the acceptance rate).

Appendix B: Relationships with the results of Cvijović et al.

In this appendix we would like to reconsider the results presented here for the chance of establishment of a mutant in a two species game, model A (section 4B above) in view of the results of obtained for a similar model by [7].
First let us take a look at the effect of environmental variations in the neutral case, i.e., when \( s_0 = 0 \). In this case our BKE takes the form (Eq. 10 with \( s_0 = 0 \))

\[
\left( \frac{1}{N} + gx(1-x) \right) \Pi''(x) + g(1-2x)\Pi'(x) = 0. \tag{B1}
\]

Since \( [\Pi'(gx(1-x) + 1/N)]' = 0 \),

\[
\Pi'(x) = \frac{c_1}{\left( \frac{1}{N} + gx(1-x) \right)}. \tag{B2}
\]

Solving this equation in the three regimes, \( x \ll 1 \), \( 1-x \ll 1 \) and \( Ngx(1-x) \gg 1 \) and matching the solutions one obtains,

\[
\Pi_{in}(x) = \frac{\ln(1+gn)}{2\ln(Ng)}, \tag{B3}
\]

so the chance of invasion for a mutant \( (n=1, \ x=1/N) \) is,

\[
\Pi_{n=1} = \frac{\ln(1+g)}{2\ln(Ng)}. \tag{B4}
\]

Eq. (B4) is equivalent to Eq. [5] of [7], up to a numerical factor. Physically this result implies that the chance of a mutant to establish increases with \( g \), in contrast with the result we have presented in section 4B. The intuitive explanation of this effect has been given by [7]: while the chance of a neutral mutant to take over the system under pure demographic noise is \( 1/N \), the chance of fixation under extremely large values of \( \delta \), say, will be \( 1/2 \) (the chance of the mutation to appear in a beneficial period) times \( 1/\gamma \) (the chance of fixation in a beneficial period) and \( 1/(2\gamma) \gg 1/N \).

However, in section 4B above we showed that in model A the chance of fixation for a beneficial mutant is a monotonously decreasing function of \( \gamma \) (or, in general, \( g \)), the strength of environmental stochasticity. Technically, \( \Pi_{n=1} \) in Eq. (14) decays with \( g \) for any value of \( s_0 \). Taking (B4) into account one realizes that for any fixed value of \( N \) and \( g \) the response to environmental variations must change sign as \( s \) becomes smaller, meaning that (14) must break down. In particular, (14) fails to converge to the neutral result (B4) when \( s_0 \to 0 \).

To address this problem one should carry more carefully the boundary layer analysis of Eq. (10). Instead of dividing the region between \( x = 0 \) and \( x = 1 \) into two regions, \( x \ll 1 \) and \( Ngx(1-x) \gg 1 \), another region, \( 1-x \ll 1 \), should be taken into account. Through this paper we have no interest in this regime because we are not interested in fixation but in establishment: in the clonal interference phase there are no fixation event, and the only interesting problem is to find the chance of a beneficial mutation to reach a macroscopic density (finite \( x \)). The third region \( 1-x \ll 1 \) is relevant only when one need to consider fixation.

Solving Eq. (10) in these three regions and matching the answers one obtains a more accurate expression that replaces Eq. (14)

\[
\Pi_{n=1}^{Model A} = \frac{1 - \frac{1}{(1+g)s_0/g}}{1 - \left( Ng \right)^{-2s_0/g}}. \tag{B5}
\]

Eq. (B5) indeed converges to (B4) when \( s_0 \to 0 \), so it provides the large \( N \) asymptotic formula for any value of \( s_0 \). Indeed, \( \Pi_{n=1}^{Model A} \) may either increase or decrease with \( g \) for different values of \( N \) and \( s \).

A closer inspection of (B5) reveals that, for any finite values of \( s_0 \) and \( g \), the denominator approaches one as \( N \to \infty \), yielding back (14), so \( \Pi_{n=1} \) always decays with \( g \) in this limit. However, 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 \( g_c \approx s_0 \ln(s_0N) \).