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Stability of two-species communities: Drift, environmental stochasticity, storage effect and selection



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ABSTRACT

The dynamics of two competing species in a finite size community is one of the most studied problems in population genetics and community ecology. Stochastic fluctuations lead, inevitably, to the extinction of one of the species, but the relevant timescale depends on the underlying dynamics. The persistence time of the community has been calculated both for neutral models, where the only driving force of the system is drift (demographic stochasticity), and for models with strong selection. Following recent analyses that stress the importance of environmental stochasticity in empirical systems, we present here a general theory of the persistence time of a two-species community where drift, environmental variations and time independent selective advantage are all taken into account.

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1. Introduction

One of the main contemporary challenges of the life sciences is to understand the factors that allow for the maintenance of biodiversity (Sachs et al., 2009; Chesson, 2000). A fundamental proposition in population genetics and community ecology, the competitive exclusion principle (Hutchinson, 1961; Stomp et al., 2011), suggests that when two genetic alleles or two biological species compete for the same resources only one species/allele will survive. Despite its theoretical importance and its firm mathematical foundations, many natural systems appear to violate this principle, allowing for coexistence of many competing species or (higher than expected) polygenic variations.

In community ecology, the simplest explanation for such a situation is resource partitioning, meaning that multiple limiting resources may give rise to a collection of species, ranging up to the number of resources, with each species excelling with respect to one resource (Tilman, 1982). However the identification of limiting resources is difficult in practice, and in some cases (tropical trees Ter Steege et al., 2013, fresh-water plankton Hutchinson, 1961; Stomp et al., 2011 and coral reef Connolly et al., 2014) the resource-partitioning mechanism seems implausible. An understanding of possible alternative coexistence-promoting mechanisms is a subject of much interest both in community ecology (Chesson, 2000) and population genetics.

Taking into account the inherent stochasticity in biological populations dynamics, one realizes that the biodiversity puzzle is, in

https://doi.org/10.1016/j.tpb.2017.11.003 0040-5809/© 2017 Elsevier Inc. All rights reserved. fact, a question about *time scales*. The dynamics of every population admits an absorbing state: once the species goes extinct, it cannot recover again. Accordingly, every biosystem suffers from a continuous loss of life forms, a process that reduces its diversity. Biodiversity equilibrates when the rate of extinction matches the rate at which new types are introduced into the system as a result of speciation or mutation events (or, for a local community, migration from a regional pool).

An important theoretical framework in which this insight is implemented is the neutral model, both in its well-mixed form (Kimura, 1985) (in genetics) and in its spatial, mainland-island version (Hubbell, 2001a; Volkov et al., 2003; Rosindell et al., 2011) in community ecology. The neutral model assumes that all species are demographically equivalent (no selective advantage) and that species abundance varies only due to genetic/ecological drift (demographic stochasticity). When two species compete under these conditions, the persistence time of the community (the time until one of them goes extinct, also known as the absorption time Ewens, 2004) is, on average, *N* generations, where *N* is the size (number of individuals) of the community. If the timescale on which new types are introduced into the system (by speciation, mutation or migration) is comparable to the persistence time, the typical number of species will be larger than one.

Recently, a series of studies showed that the abundance variations in empirical ecological communities are much stronger than those predicted by the neutral model (Kalyuzhny et al., 2014b, a; Chisholm et al., 2014). This appears to reflect the presence of *environmental* stochasticity, i.e., the random variations in species relative fitness caused by fluctuations in exogenous factors like precipitation, temperature, predation pressure and so on (Lande

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et al., 2003). Demographic noise accounts for the stochastic factors that affect each individual independently, so the average fitness of a population is fixed and abundance fluctuations per generation scale like the square root of population size. Conversely, under environmental stochasticity the fitness of all individuals in a certain population fluctuates in a correlated manner, leading to much stronger abundance variations.

Based on this observation, a time-averaged neutral theory of biodiversity has been suggested (Kalyuzhny et al., 2015; Danino et al., 2016), where environmental stochasticity affects the system but species are still symmetric since each species' fitness, *when averaged over time*, is identical. Again, species go extinct at a certain rate, now determined by both demographic and environmental stochasticity, and biodiversity reflects the balance between extinction and speciation (or migration) rates. This model has been shown to fit quite nicely the static and dynamic characteristics of a (local) community of tropical trees (Kalyuzhny et al., 2015; Fung et al., 2016); both the species abundance distribution and the abundance variations are similar to the predictions of the model as obtained from numerical simulations.

The inclusion of environmental stochasticity into the model makes it necessary to revisit the timescale problem. Environmental stochasticity is stronger than drift, and overshadows its effect in large abundance populations. Environmental stochasticity at first sight appears to be a destabilizing factor: it increases the amplitude of abundance variations and hence shortens the time until a population reaches a low-abundance state and goes extinct. The naive expectation, thus, is that environmental stochasticity shortens the persistence time, though one would like to quantify this argument and to find the *N* dependence explicitly.

However, under some circumstances environmental stochasticity may become a *stabilizing* mechanism, as suggested by Chesson and collaborators (Chesson and Warner, 1981; Hatfield and Chesson, 1989, 1997). These authors show that environmental variations may enhance the chance of invasion of low-abundance species via the *storage effect*: rare species, when compared with common species, have fewer per-capita losses when their fitness is low and more gains when their fitness is high. As a result, the system may admit stochastic persistence: every species' abundance fluctuates, but all are peaked about a finite value by a noise-induced stabilizing force (see Schreiber, 2012 for a detailed discussion of the persistence properties in models without demographic noise).

Chesson and coworkers introduced the *lottery model*, a minimal model that captures the essence of the storage effect, and analyzed its stability properties. However, they considered a system with pure environmental stochasticity and without demographic stochasticity. In such a system there is no extinction per se, as population density may take arbitrarily small values. Accordingly, the criteria they used to define a stable equilibrium was the normalizability of the probability density function. This strategy did not allow them to calculate persistence times, making it impossible to analyze diversification rates.

In a recent paper (Hidalgo et al., 2017), Hidalgo et al. considered the two-species community persistence problem in the presence of environmental stochasticity, with and without storage. Like (Chesson and Warner, 1981), they analyzed the dynamics of a twospecies community with pure environmental stochasticity, such that the number of individuals belonging to each of the species is not necessarily an integer. For a community of *N* individuals, extinction of a species occurred, in their work, when that species' fraction of the population becomes smaller than 1/N. Looking at the system under dichotomous (telegraphic) environmental stochasticity, they were able to calculate the large *N* asymptotic behavior of extinction times for a time-averaged-neutral community. This approximation, the replacement of demographic noise by a cutoff at threshold value of 1/N, corresponds to the neglect of all its stochastic aspects, keeping only the absorbing state at zero. To close the gap between the asymptotic behavior at large N and the regimes where demographic noise is important, Hidalgo and coworkers suggested the existence of (one or two parameter) scaling functions and provide numerical evidence to support their conjecture.

Here we solve the persistence time problem in all its glory, taking into account explicitly both demographic and environmental stochasticity. This allows us to extend the theory suggested by Hidalgo et al. in the following senses:

- 1. An explicit, closed form for the scaling functions (in terms of a single or a double integral) is derived, so the answer covers all the range of parameters. In particular, our formulas converge to the pure demographic limit when the environmental stochasticity vanishes.
- 2. The expressions suggested in Hidalgo et al. (2017) for the large *N* limit are recovered, but we can calculate also subleading terms in this asymptotic series. This allows us to identify the parameter region where the asymptotics is accurate, and to suggest simple analytic approximations that cover a much wider region of parameters.
- 3. We can calculate the persistence time for a single mutant. This is an important quantity, as it sets the threshold for clonal interference and may be relevant to the small island effect in island biogeography (see next section).

Moreover, we have extended the work of Hidalgo et al. (2017) to include the case where one species has on average a selective advantage with respect to the other species, superimposed on the environmental variations.

This paper is organized as follows. In the next section we provide a few basic intuitive arguments and a summary of the main results. Section 3 deals with the case of pure demographic noise, in Section 4 we consider the case of demographic and environmental stochasticity (where fitness fluctuates in time, but the mean fitness difference is zero) without storage effect, and in 5 the case with storage effect. Section 6 is devoted to the effect of selection (when the mean relative fitness is nonzero) on persistence time when it acts against the storage mechanism, and is followed by a discussion section. For the sake of completeness we describe in Appendices the results for a system with selection and pure demographic noise (Appendix B) and selection with both environmental and demographic noise, but without storage (Appendix C).

2. Intuitive arguments, glossary and summary of the main results

In this section we explain the main issues considered in this paper, introduce the notations, provide a glossary (see Table 1) and briefly sketch the main results.

Throughout this paper we consider two "species" (genetic types, zoological species, bacterial strains) that compete with each other for, say, a single limiting resource. When the demographic rates of these two species are equal and the strength of the intraspecific competition is equal to the strength of the interspecific competition, the model is neutral (Hubbell, 2001b) and the dynamics is driven solely by stochastic effects. The analysis of this case is usually based on a zero-sum game approximation, assuming that the total number of individuals is fixed in time and so neglects the short-lived fluctuations that may change the community size (Volkov et al., 2003). We adopt this approximation even for the cases where one of the species has a (transient or permanent) selective advantage: the number of individuals in the community is kept fixed, and selection determines the instantaneous tendency of the abundance of one species to grow at the expense of its opponent and vice versa.

2.1. Persistence time: definition and the importance of initial conditions

We define the persistence time (also known as the absorption time Ewens, 2004), of a two species community as the mean time until one of the species goes extinct. To account for the effect of demographic stochasticity we implement a set of individual based models. In each elementary step of these models one individual is chosen at random to die and is removed, with its slot being captured by an offspring of another individual, chosen with some probability that reflects its (instantaneous) relative fitness. Such a stochastic birth-death process leads, inevitably, to the extinction of one of the species, and our goal is to calculate how much time, on average, it takes for the system to reach this monomorphic state, given the size of the community, N, and the initial conditions, in which species 1, say, is represented by n_0 individuals and species 2 has $N - n_0$ individuals. Time is measured in units of generations, where a generation is defined as N elementary death-andrecruitment steps.

We do not calculate here the fixation time, which is defined as the average time it takes a specific species to reach an abundance of *N* conditioned on its success. The quantity we are looking at measures the persistence time of a community (i.e., the time to fixation or loss).

While we provide expressions for any initial condition, two special cases are of particular importance. One is the case of a single mutant introduced into a system, i.e., $n_0 = 1$, $N - n_0 =$ N-1. This is the relevant case when a new type appears due to a single mutation/speciation event, or when the system is subject to weak immigration from a regional pool. The biodiversity (species richness, genetic polymorphism) of such a system depends on the balance between the rate of appearance of new types (rate of mutation, migration, or speciation) and the average time it takes for the single mutant abundance to reach either zero or N. If the rate of mutation is small (in units of inverse persistence time), the community will be monotypic most of the time. If the rate is high, the typical state has more than one species, and thus the ratio between these two rates determines the threshold for clonal interference (Gerrish and Lenski, 1998). By the same token, a recently proposed explanation for what is known (in island biogeography) as the small island effect suggests that the number of niches per island is fixed and for small islands the rate of absorption is smaller than the rate of immigration (Chisholm et al., 2016). Under these assumption, an island is "small" as long as the immigration rate is smaller than the inverse of the persistence time calculated here.

Another interesting scenario is the case where both n_0 and $N - n_0$ are initially large. This may happen when the community is subject to strong invasion, when speciation occurs allopatrically and then the two groups mix again, for protracted speciation (Rosindell et al., 2010) or in experiments in which two bacterial strains or two vegetation species are mixed (Jiang and Morin, 2007). One may get insight into the persistence time in this case by identifying the initial state for which this time is maximized (e.g., in a symmetric system, this will be the initial state $n_0 = N/2$) and calculating the persistence time for this state. In what follows we provide simple expressions for these two cases: the maximum value of the expected persistence time and the expected persistence time for a single mutant.

2.2. Demographic stochasticity (drift) and the neutral model

Demographic stochasticity is defined, in our models, as those aspects of stochasticity that affect individuals in an uncorrelated manner. The origin of these stochastic forces is not important: they may reflect genetic variations, fluctuations of the local environment or any other factor; what matters is that their effect on the reproductive success of a given individual is independent of their effect on other individuals that belong to the same species.

When the two species in the community are (on average) demographically identical, and population variations are driven solely by demographic noise (in our zero-sum model, this implies that one individual is chosen to die and another is chosen to reproduce, both choices are random and the species affiliation does not play any role), the dynamics is known as *neutral*. Under neutral dynamics, the maximum value of the expected persistence time (measured in units of generations, see below) is known to be proportional to *N* (Crow et al., 1970). We review the features of the neutral model in Section 3.

2.3. Selection

When one species has a selective advantage with respect to the other, its chance to capture the whole community is, of course, larger. In the game considered here we always kill one individual at random, with no distinction between species, but if species 1, say, has a selective advantage, the per capita chance of an individual of species 1 to capture the empty slot is larger than the chance of a species 2 individual. The difference between these two per capita chances is proportional to the selection parameter η_0 .

On average, a species with selective advantage grows exponentially, so the time it takes to reach *N* from $n_0 = 1$ will scale, deterministically, like $\ln(N)/\eta_0$ (Crow et al., 1970). This behavior is preserved under demographic noise, as demonstrated in Appendix B.

2.4. Environmental stochasticity

This paper is focused on the effect of environmental stochasticity (fitness fluctuations) on the persistence time. In contrast with demographic noise, environmental stochasticity reflects those aspects of the environmental variations that affect *coherently* the reproductive success of all the individuals that belong to a certain species. As the environmental conditions vary, the relative fitness of species may change. Accordingly, for large populations the effect of environmental stochasticity is more important than the drift (Lande et al., 2003). However, without demographic stochasticity there is no extinction; to calculate extinction times one must either consider explicitly the demographic noise, as we are doing here, or impose a threshold on the density at the level of one individual, as done in Hidalgo et al. (2017).

When both species have the same average fitness, but the fitnesses fluctuate randomly so that at any single moment one of them is superior (i.e., species fitness varies in time, but when averaged over time the two species are still symmetric) we speak about a system under environmental stochasticity and characterize it by two quantities: the squared amplitude of fitness variations, γ^2 , and the correlation time of the environment (in units of generations), δ . Environmental stochasticity may be superimposed on an average fitness advantage of one species, and in that case we make a distinction between selection (the time independent component of the relative fitness, denoted by η_0) and stochasticity (zero-mean fitness fluctuations). For clarity, throughout this paper we use the word "selection" when we refer to the case where the time-averaged (logarithmic) fitness advantage is nonzero, while "environmental stochasticity" refers to zero-mean fluctuations of this quantity.

The simplest way to think about a system driven by environmental stochasticity (with no selection and no demographic noise) is to consider it as a random walk of the logarithmic relative abundance. If x = n/N is the fraction of one species 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"

 $\gamma^2 \delta$. Since the typical time needed for a random walker to cross a distance *L* scales like L^2 , one expects that the maximum persistence time for a community of size *N* (so $-\ln(N) < z < \ln(N)$ if extinction is declared when *x* reaches 1/N) will scale like $\ln^2(N)$ for large *N*. This asymptotic behavior was found by Hidalgo et al. (2017). Here, in Section 4, we provide the expression for any *N* and any initial conditions (Eqs. (15) and (16)), calculate the leading corrections to the large *N* result and identify the region in which this log squared asymptotics is valid (Eqs. (18) and (20)). We also show that the result for a single mutant initial condition has a different scaling (Eq. (21)) and explain why this happens.

2.5. Noise induced stabilization: the storage effect

Environmental stochasticity in this model is thus seen to be a destabilizing factor, as it increases the amplitude of abundance fluctuations and shortens the persistence timescale from N generation (with pure demographic noise) to $\ln^2(N)$. However, under some circumstances the environmental stochasticity stabilizes the system and increases substantially the persistence time. This possibility was discovered by Chesson and coworkers (Chesson and Warner, 1981; Chesson, 1994), and is known as the storage effect.

Let us demonstrate the stabilizing effect of environmental stochasticity using a simple version of the Chesson-Warner lottery game. To do that, one may think about individuals as trees, say, and assume that the seed bank in the soil reflects the abundance of each species. Upon death of an individual one of the seeds is chosen to capture its location as an adult tree with a chance proportional to its fitness, and so the overall chance of a species to increase its population reflects both its abundance and its instantaneous fitness, superimposed nonlinearly. As an example, let us think about a "winner takes all" case, where the species with higher fitness wins the empty slot for certainty. Starting with 8 red individuals and 2 green in a community of 10, the chance to end up with 7 red and three green is 0.4 (a red is killed with probability 0.8, the green captures the slot with probability 1/2 since it is preferred half of the time) while the chance to end up in the 9:1 state is only 1/10. Rare species have a larger chance to grow in abundance just because they are rare.

The persistence time for a system with environmental stochasticity and storage effect was considered by Hidalgo et al. (2017), who suggested that for large *N* it scales like $N^{1/\delta}$. Our analysis provides an expression for any *N* and any initial condition (Eq. (32)), with an analysis of the large *N* behavior and the crossover to the $N^{1/\delta}$ regime (Eq. (35)). We also consider the same problem for a single mutant (Eq. (37)), showing that in this case the scaling of the persistence time with *N* is also $N^{1/\delta}$. Moreover, the maximum persistence time and the persistence time of a system with a single mutant differ only by a factor of $\gamma^2/2$.

2.6. The interplay between stochasticity and selection

The situations described so far correspond to the standard neutral model (perfect demographic equivalence, zero fitness differences between species and individuals) and to the time-averaged neutral model (TNTB) (Kalyuzhny et al., 2015; Danino et al., 2016), where the species have the same fitness on average, but at each moment one species has higher fitness. In both cases, stochasticity (demographic or environmental) is the only driver of abundance variations.

However, the generic scenario appears to be the case where a time independent selective advantage to one of the species is superimposed on environmental variations that may give instantaneous superiority to its opponent (Bell, 2010).

We consider this situation, with and without storage effect, in Section 6 and Appendix C. For the case without storage we provide the general formula in (C.5), showing that in the large *N* limit, selection alone determines the persistence time (Eq. (C.9)). With storage, the situation is much more interesting: there is a scaled selection parameter $\tilde{s} = 2\eta_0/\gamma^2$, and as long as this parameter is smaller than $(1 - \delta)$, noise induced stabilization wins and the time to extinction grows superlinearly with *N* (like $N^{(1-\bar{s})/\delta}$). These results are summarized in Eqs. (41) (general formula) and (49) (large *N* asymptotics).

To allow for a comparison, the results for the main models considered below are summarized in Table 2. The table shows only the leading asymptotic behavior at large N, together with references to the appropriate formulas in the text.

3. Neutral dynamics with pure demographic stochasticity (drift)

To set the framework for the next sections and to clarify a few technical points, let us begin by considering the already studied (Crow et al., 1970; Karlin and Taylor, 1981) case of a two species system with fixed community size N and pure demographic noise. Species #1 is represented by n individuals and species #2 by N - n individuals. During each elementary step one individual (chosen at random) dies (is removed from the community, leaving a gap), and an offspring of another (again, randomly chosen) individual, is recruited into this gap. We fix the time unit as a generation, so that the duration of each elementary birth–death event is 1/N.

If the birth-death event involves two conspecific individuals (one dies and the offspring of the other captures the vacant gap) the frequencies of the two species remain fixed. The chance of an interspecific substitution (an elementary event in which the frequencies of the two species are modified) is,

$$F_n = F_{N-n} = \frac{2n(N-n)}{N(N-1)},$$
(1)

where in the continuum limit we use x = n/N and the approximation,

$$F(x) = 2x(1-x),$$

since $N \gg 1$ such that $N - 1 \approx N$.

Without loss of generality, let us focus on the first species, represented at t = 0, say, by n_0 individuals. Eventually the system must reach one of the two absorbing states, n = 0 or n = N. The mean persistence time of the two species community (time until fixation of one of the two species, starting from n_0), T_{n_0} , satisfies the backward Kolmogorov equation (BKE) (Redner, 2001),

$$T_{n_0} = (1 - F_{n_0}) \left(T_{n_0} + \frac{1}{N} \right) + F_{n_0} \left(\frac{1}{2} T_{n_0 - 1} + \frac{1}{2} T_{n_0 + 1} + \frac{1}{N} \right), \quad (2)$$

or equivalently (from now on we refer to n_0 simply as n, since Eq. (2) does not involve explicitly the dynamics of the system),

$$-\frac{1}{N} = F_n \cdot \left[-T_n + \frac{1}{2}T_{n-1} + \frac{1}{2}T_{n+1} \right]$$
(3)

with the boundary conditions

$$T_0 = T_N = 0. \tag{4}$$

To write the BKE (3) as a differential equation, we consider $x \equiv n/N$ as a continuous variable and expand $T(x \pm 1/N)$ to second order, obtaining

$$-\frac{N}{x(1-x)} = \frac{\partial^2 T(x)}{\partial x^2}.$$
(5)

Integrating twice and plugging in the boundary conditions (4) one finds,

$$T(x) = -N[x\ln(x) + (1-x)\ln(1-x)],$$
(6)

Glossary.	
Term	Description
Ν	Number of individuals in the community (both species).
n	Number of individuals belonging to species $1 (N - n belong to species 2)$.
x	Fraction of species 1, $x = n/N$. $(1 - x$ is the fraction of species 2)
τ	Correlation time of the environment, measured in units of elementary steps.
δ	Correlation time of the environment, measured in generations.
T(x)	Mean persistence time for a two species system at <i>x</i> , when the environment is fixed in time.
<i>S</i> (<i>x</i>)	Mean persistence time for a two species system at <i>x</i> , when the environment is fluctuating between two states, and the average is taken over both initial conditions and histories.
η_0	The time-independent component of the fitness.
γ	The amplitude of the fluctuating component of the fitness.
$G \equiv N \delta \gamma^2 / 2$	Scaled environmental stochasticity.
$\tilde{s} \equiv 2\eta_0/\gamma^2$	Scaled selection.

Table 2 Main results.

Stochasticity	Persistence time of a single mutant	Maximum persistence time	Maximum persistence time with selection
Pure demographic	ln N	Ν	ln N
	Section 3, Eq. (8)	Section 3, Eq. (7)	Appendix B, Eq. (B.5)
Demographic + Environmental no storage	ln N	ln ² N	ln N
	Section 4, Eq. (21)	Section 4, Eq. (19)	Appendix C, Eq. (C.9)
Demographic + Environmental weak storage	$N^{1/\delta}$	$N^{1/\delta}$	$N^{(1-\tilde{s})/\delta}$
	Section 5, Eq. (36)	Section 5, Eq. (37)	Section 6, Eq. (50)

meaning that the persistence time, for every fixed x, grows linearly with *N*. Fig. 1 demonstrates the validity of Eq. (6) when tested against two types of numerical results: a numerical solution of Eq. (2), written as $T_n = 1/N + \sum_m M_{mn}T_m$ and solved by matrix inversion, and a direct Monte-Carlo (MC) simulation of the underlying neutral process, averaged over many realizations. The details of these numerical techniques are given in Appendix A.

Table 1

Two important features of (6) are the maximum persistence time obtained at x = 1/2,

$$T(1/2) = N \ln(2), \tag{7}$$

and the persistence time of the two species community, when one species is initially represented by a single individual,

$$T(1/N) = \ln(N). \tag{8}$$

If ν is the per-birth chance of a single individual of a new type to enter the system (for example, the chance of a newborn individual to be a mutant, or the originator of a new species, or the chance that an immigrant from a regional pool, belonging to a different type, replaces a dead individual), then the typical number of species in the community will be unity as long as $\nu N \ln(N) < 1$ (so that when a new type appears, it typically goes extinct or takes over the whole community before the next speciation or migration event). The system typically will be found in a state with more than one species if $\nu N \ln(N) > 1$. The value $\nu_c = 1/[N \ln(N)]$ is thus the threshold for *clonal interference* (Gerrish and Lenski, 1998; Park and Krug, 2007) and for the small island effect (Chisholm et al., 2016).

Actually, in this simple, pure demographic, case, even the transition to the continuum is unnecessary. One can instead solve the difference equation (3) exactly by writing it as a first order difference equation for $W_n \equiv T_n - T_{n-1}$,

$$-\frac{N-1}{n(N-n)} = W_{n+1} - W_n.$$
 (9)

Accordingly,

$$W_n = W_1 - \left(1 - \frac{1}{N}\right) \sum_{k=1}^{n-1} \left(\frac{1}{k} + \frac{1}{N-k}\right).$$

Deriving T_n in the same way and applying the boundary condition $T_0 = 0$ and $T_N = 0$ one finds,

$$T_n = \left(1 - \frac{1}{N}\right)(NH_N - nH_n - (N - n)H_{N-n}),$$

where $H_n \equiv \sum_{k=1}^n k^{-1}$ is the *n*th harmonic number. This expression converges to Eq. (6) in the large *N* limit. The maximum persistence time is,

$$T_{N/2} \approx N\left(\ln(2) - \frac{1}{2N} + \mathcal{O}\left[\frac{1}{N^2}\right]\right),\tag{10}$$

so the exact solution differs from the continuum result, Eq. (7), by a negligible factor in the large N limit.

4. Environmental stochasticity without storage mechanism

In this section we consider a similar Moran (individual based) process, with the addition of fitness variations caused by environmental fluctuations characterized by the quantities ν and δ . The 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 random individuals fighting for a piece of food, the winner reproduce and the loser dying. In our zero-sum model, in each elementary step two individuals (*i* and *j*) are chosen at random for a duel. If both individuals belong to the same species, the result of the duel does not affect the species' abundances. In case of an interspecific duel, the chance of species 1 to win is $1/2 - \gamma/4$ when the environment favors species 2, and $1/2 + \gamma/4$ when the environment favors species 1 (dichotomous noise). When $\gamma = 0$, the pure demographic game considered in the last section is recovered. Since both species have the same average fitness as the selective force fluctuates in time (environmental stochasticity), this situation corresponds to the time averaged neutrality considered in Kalyuzhny et al. (2015), Danino et al. (2016) and Hidalgo et al. (2017).

In our model, after each elementary step the chance of the environment to stay in the same state is taken as $1 - 1/\tau$, and the chance of the environment to flip (i.e, $\pm \gamma \rightarrow \mp \gamma$) is $1/\tau$. Accordingly, the environmental fluctuations are characterized by



Fig. 1. A comparison between the results of a Monte-Carlo simulations, numerical solution of the backward Kolmogorov equation (see methods in Appendix A) and the analytic results (6) for T(x). In the left panel T(x) is plotted against x for a system with N = 100, where the MC simulation reflect an average over 10 000 runs. In the right panel the maximum lifetime T(1/2) is plotted as a function of N (red filled circles) and is compared with the $T = N \ln(2)$ relationships predicted from (6) for x = 1/2. In both cases the agreement is excellent.

two parameters: γ , the fluctuation amplitude and $\delta \equiv \tau/N$, the environmental correlation time (in units of a generation). 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 herein are quite generic.

For a fluctuating environment, we should define again the persistence time. If, at t = 0, species #1 is represented by *n* individuals *and* the system is in the $+\gamma$ state, the persistence time is T_n^+ , while if at t = 0 the system is in the $-\gamma$ state we denote the persistence time by T_n^- . The BKE (with $q \equiv 1/2 - \gamma/4$) reads,

$$T_{n}^{+} = \frac{1}{N} + \left(1 - \frac{1}{\tau}\right) \left\{ F_{n} \left[qT_{n+1}^{+} + (1 - q)T_{n-1}^{+} \right] + [1 - F_{n}]T_{n}^{+} \right\} \\ + \frac{1}{\tau} \left\{ F_{n} \left[qT_{n-1}^{-} + (1 - q)T_{n+1}^{-} \right] + [1 - F_{n}]T_{n}^{-} \right\}$$
(11)

$$T_n^- = \frac{1}{N} + \left(1 - \frac{1}{\tau}\right) \left\{ F_n \left[q T_{n-1}^- + (1-q) T_{n+1}^- \right] + [1 - F_n] T_n^- \right\} \\ + \frac{1}{\tau} \left\{ F_n \left[q T_{n+1}^+ + (1-q) T_{n-1}^+ \right] + [1 - F_n] T_n^+ \right\}.$$

Defining $S_n \equiv (T_n^+ + T_n^-)/2$, $\Delta_n \equiv (T_n^+ - T_n^-)/2$, moving to the continuum limit $x \equiv n/N$ and expanding $T(x \pm 1/N)$ to the order in a Taylor series as above, one finds:

$$\frac{2}{\tau}\Delta = \left(1 - \frac{2}{\tau}\right)x(1 - x)\left[\frac{-\gamma}{N}S' + \frac{\Delta''}{N^2}\right]$$
(12)
$$-1 = x(1 - x)\left(\frac{S''}{N} - \gamma\Delta'\right)$$

where the derivatives are with respect to *x*.

If $\tau = 2$ (i.e., $\delta = 2/N$), the chance of the environment to switch from $\pm \gamma$ to $\mp \gamma$ after each elementary step is 1/2. In this limit the environmental stochasticity becomes demographic: the outcome of each duel is determined by two independent drawings of a random variable, one that dictates the environmental conditions and the other determines the result given these conditions, so the net chance to win a duel is again 1/2 with no correlations in time. This can be seen from Eqs. (12): the r.h.s. of the upper equation is zero, meaning that $\Delta = 0$, and the lower equation reduces to (5).

In most of the realistic scenarios one would like to ensure that the persistence time of the environment is independent of the size of the community, i.e., to assume that δ is fixed, and so, in the large N limit, $2/\tau$ is negligible. In this case, (12) takes the form,

$$-\gamma S' + \frac{\Delta''}{N} = \frac{2\Delta}{\delta x(1-x)}$$

$$\frac{S''}{N} - \gamma \Delta' = -\frac{1}{x(1-x)}.$$
(13)

Using a (numerically inspired) dominant balance argument, we discovered that for reasonably large *N* the Δ''/N term is negligible in the first equation (see further discussion of this point in the last paragraph of this section). Solving the first equation for Δ and plugging it into the second, we obtain an inhomogeneous, first order ODE for *S'*. From symmetry, *S*(*x*) peaks at *x* = 1/2, meaning that *S'*(1/2) = 0; using that as a boundary condition one obtains:

$$S' = -\frac{N \ln\left(\frac{x}{1-x}\right)}{1+N\delta\gamma^2 x(1-x)/2}$$
(14)
$$\Delta = \frac{N\delta\gamma x(1-x) \ln\left(\frac{x}{1-x}\right)/2}{1+N\delta\gamma^2 x(1-x)/2}.$$

S is the average persistence time, when one averages over both initial conditions (i.e., starting at a certain *x*, when half of the realizations the environment favors species 1 at t = 0) and fluctuation histories. To calculate *S* we integrate *S'*, invoking the boundary condition S(0) = 0 (which by symmetry implies S(1) = 0 as well), so that

$$S(x) = -N \int_0^x dt \frac{\ln\left(\frac{t}{1-t}\right)}{1 + Gt(1-t)},$$
(15)

where

$$G \equiv N \delta \gamma^2 / 2$$

is the ratio between the strength of environmental stochasticity, $\gamma^2 \delta/2$, and the strength of the demographic noise 1/N. This parameter controls the transition between the demographic noise dominated regime and the environmental stochasticity dominated regime, as we shall demonstrate immediately. The general form of Eq. (15) is $S(x) = N\mathcal{F}(G, x)$, so $S(1/2) = N\mathcal{F}(G)$, in agreement with the prediction of Hidalgo et al. (2017) of a one parameter scaling function.

Eq. (15) is a closed form expression for S(x), and one may easily evaluate this integral numerically. Moreover, an explicit solution may be written in a form of the dilogarithm functions (Abramowitz and Stegun, 1964) $Li_2(x) \equiv -\int_1^x dt \ln(t)/(t-1)$:

$$S(x) = -\frac{N}{\sqrt{G(4+G)}} \left[2 \operatorname{atanh} \left(\frac{\sqrt{G(4+G)}(1-x)}{2+G(1-x)} \right) \ln(1-x) + 2 \operatorname{atanh} \left(\frac{\sqrt{G(4+G)}x}{2+Gx} \right) \ln x - \operatorname{Li}_2 \left(1 - \frac{2(1-x)}{G+\sqrt{G(4+G)}} \right) + \operatorname{Li}_2 \left(1 + \left(G + \sqrt{G(G+4)} \right) (1-x)/2 \right) \right]$$

$$-\operatorname{Li}_{2}\left(1 - \frac{2x}{G + \sqrt{G(4+G)}}\right) + \operatorname{Li}_{2}\left(1 + \left(G + \sqrt{G(G+4)}\right)x/2\right) - \operatorname{Li}_{2}\left(1 + \left(G + \sqrt{G(G+4)}\right)/2\right) + \operatorname{Li}_{2}\left(1 + \frac{G - \sqrt{G(G+4)}}{2}\right)\right].$$
(16)

To understand intuitively this result, it is better to consider the asymptotic behavior of the maximum persistence time, S(1/2), as obtained from the integral (15), in the limits of small and large *G*. As long as $G \ll 1$, one can neglect the second term in the denominator to get

$$S(1/2) = -\int_0^{1/2} N \ln\left(\frac{x}{1-x}\right) \, dx = N \ln(2),\tag{17}$$

i.e., the pure demographic result (7). If $G \gg 1$ one may define $1/G \ll \zeta \ll 1$ and use asymptotic matching (Bender and Orszag, 1999) to obtain the leading behavior:

$$S(1/2) \approx -N \int_{0}^{\zeta} \frac{\ln(x)}{1+Gx} dx - \frac{N}{G} \int_{\zeta}^{1/2} \frac{\ln\left(\frac{x}{1-x}\right)}{x(1-x)} dx$$
$$\approx N \left[\frac{\ln^{2}(G) + \pi^{2}/3}{2G} + \mathcal{O}\left(\frac{\ln^{2}(G)}{G^{2}}\right) \right].$$
(18)

Fig. 2 demonstrates the validity of our results. The agreement between S(x) as obtained from Eq. (16) and the numerical simulations is quite good, and the dependence of S(1/2)/N on *G* is shown to satisfy (16).

As Hidalgo and coworkers (Hidalgo et al., 2017) suggested, the large N asymptotic behavior of the persistence time scales, for this scenario, like

$$S(1/2) \sim \ln^2 N,$$
 (19)

and the general behavior is described by a function of the form $S(1/2) = N\mathcal{F}(G)$, where $\mathcal{F}(G)$ approaches unity when the environmental stochasticity vanishes $(G \rightarrow 0)$ and $\ln^2(G)/G$ when *G* is large. Our expression (16) provides the explicit form of the required scaling function, with the correct asymptotic behaviors (Eqs. (17) and (18)).

The asymptotic matching analysis and Eq. (18) allows us to identify the large *N* scaling regime, where the $\ln^2(G)$ term is much bigger than the first correction. This happens when,

$$N \gg \frac{2e^{\pi/\sqrt{3}}}{\delta\gamma^2} \approx \frac{12.25}{\delta\gamma^2}.$$
(20)

Now let us consider the limitations of the general scaling analysis. As seen in Fig. 2, when *G* approaches zero with *N* fixed (meaning that the environmental stochasticity parameter $\delta \gamma^2$ is decreasing) the system approaches smoothly the demographic noise limit $S(1/2)/N = \ln(2)$. However, when the noise is kept fixed and *N* decreases (filled red circles) there are deviations, since the demographic noise limit admits small *N* corrections (10), and the scaling hypothesis breaks down. Thus, the maximum deviation is $-1/2N = -\gamma^2 \delta/4G$ which, for fixed *G*, grows with δ .

Another limitation of the general scaling comes from the large δ limit. As seen in Appendix B, the persistence time under a timeindependent selective force (i.e., when η stays fixed at η_0) scales as $\ln(N)/\eta_0$. This implies that, if $\delta \gg \ln(N)/|\gamma|$, absorption may take place before the environment has a significant chance to change. Indeed our numerics shows that, in this regime, the predictions of this section are violated and one should stick to the $\ln(N)/|\gamma|$ estimation. A surprising outcome of (16) is the persistence time of the system with a single initial mutant, S(1/N). Evaluating (16) for x = 1/N and approximating it for large *N*, we get

$$S(1/N) = \frac{\ln(1 + \gamma^2 \delta/2)}{\gamma^2 \delta/2} \ln(N).$$
 (21)

This result implies that in the large *N* limit, as long as the noise strength $\gamma^2 \delta/2$ is small, the clonal interference threshold is *the same* for this model and for a model with pure demographic stochasticity. One may understand this result intuitively by looking at the process as a random walk in the log-abundance space (Kessler et al., 2015). The first passage probability at *t* scales like $t^{-3/2}$ with a cutoff at $\ln^2(N)$, so the average lifetime, starting at one, is $\ln(N)$.

Finally, we would like to discuss the dominant balance argument that allows us to neglect the Δ''/N term in the first equation of (13). Taking the solution for Δ from Eq. (14) one may calculate Δ''/N and compare it with $\gamma S'$. It turns out that for x of order one, $\Delta''/(N\gamma S')$ approaches zero as $G \to \infty$. Even in the limit $x \to 1/N$, $\Delta''/(N\gamma S') \to \gamma^2 \delta^2/2$ (the same is true in the other limit x = 1 - 1/N). Accordingly, as long as $\gamma^2 \delta^2 \ll 1$, the Δ''/N term is negligible with respect to the other two terms for all the relevant values of x.

5. Environmental stochasticity with storage effect

As discovered by Chesson and collaborators (Chesson and Warner, 1981; Hatfield and Chesson, 1989, 1997), the introduction of environmental stochasticity into the system may induce an attractive force that stabilizes the system. Even if the environmental fluctuations are "neutral" (i.e., the fitness of both species, when averaged over time, is the same), they may support the invasion (and recovery) of low abundance species. Accordingly, one expects that the persistence time of the system is large compared to the O(N) dependence of the pure demographic noise case. In this section we consider this scenario for a two-species community with dichotomous noise.

The conditions under which this "storage effect" takes place, and its dependence on the parameters of the system, were considered by us in Danino et al. (2016). Here we would like to find the persistence time obtained from this dynamics. We have chosen an individual based version of the dynamics of the Chesson– Warner "lottery game" (Chesson and Warner, 1981). These authors have analyzed the problem without demographic stochasticity, so extinction and fixation were not allowed, while here the game is analyzed with demographic stochasticity.

For the sake of concreteness, let us consider a forest with N trees that belong to two different species. Every tree produces the same number of seeds, such that the density of seedlings (of a given species) per unit area reflects the relative abundance of the species' trees in the forest. During each elementary step, one tree is chosen at random to die, and the seedlings compete to fill the vacant site. The environmental conditions determine the fitness of these seedlings: if there are n trees of species 1 and N - n trees of species 2, the chance of species 1 to capture an empty slot, P_1 , is proportional to the number of seedlings weighted by their fitness. Here we take,

$$P_1 = \frac{n}{n + \rho(N - n)} = \frac{x}{x + \rho(1 - x)},$$
(22)

where ρ measures the relative fitness of species 2: if $\rho = 1$ the chance of a species to fill the gap is proportional to its relative abundance in the forest, and the game reduces to two species dynamics with pure demographic stochasticity. When $\rho > 1$ species 2 is preferred as its per seedling chance to take over the gap is larger, while if $\rho < 1$ this chance is smaller. Clearly, the chance of species 2 to capture the slot is $1 - P_1$.



Fig. 2. A comparison between the results of a Monte-Carlo simulations, numerical solution of the BKE and the analytic results (16) for *S*(*x*) is presented in the left panel. Results are depicted for a system with N = 1000, $\gamma = 0.2$ and $\delta = 0.1$, where the MC lifetimes were averaged over 10 000 runs. In the right panel we compare the maximum lifetime of the system, *S*(1/2), with the predictions of Eq. (16), testing both the accuracy of this formula and the general scaling hypothesis suggested in Hidalgo et al. (2017). Four sets of results, obtained using a numerical solution of the master equation, are presented. Green squares are the results for N = 2000, $\gamma = 0.1$ and δ from 2.5 $\cdot 10^{-3}$ to 0.1. Blue circles are for N = 2000, $\delta = 0.1$ and γ from 0.01 to 0.1. Red (open and filled) circles represent results with varying N with $\delta = 0.1$: for the open, $\gamma = 0.2$ and N runs from 70 to 3000, while for the filled circles $\gamma = 0.1$ and N is between 50 and 2000. Clearly, the analytic prediction and the results are in perfect agreement as long as N is sufficiently large. For small N (filled red) one may identify small deviations from the theoretical prediction and a violation of the scaling hypothesis. The magnitude of these discreteness induced corrections for N = 50 is about 0.01, in agreement with the O(1/2N) scaling predicted in Eq. (10). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Again we are interested in the case where $\ln(\rho)$, the log-fitness, takes the values $\pm \gamma$, where γ measures the strength of the environmental fluctuations. As in the last section, the chance to switch between plus and minus γ is $1/\tau$ per elementary step, so $\delta \equiv \tau/N$ is the environment correlation time as measured in units of a generation time.

Defining P_1^+ and P_1^- as the values of P_1 in the $\pm \gamma$ states, correspondingly, one realizes that the chance of species 1 to increase its abundance during an elementary step is $(1 - x)P_1^+$ when the environment favors it and $(1 - x)P_1^-$ when the fitness of species 2 is higher. The backward Kolmogorov equation then reads,

$$T^{+}(x) = \frac{1}{N} + \left(1 - \frac{1}{\tau}\right) \left\{ \left[(1 - x)P_{1}^{+}T^{+}(x + 1/N) + x(1 - P_{1}^{+})T^{+}(x - 1/N) \right] + \left[1 - (1 - x)P_{1}^{+} - x(1 - P_{1}^{+}) \right]T^{+}(x) \right\} \\ + \frac{1}{\tau} \left\{ \left[(1 - x)P_{1}^{-}T^{-}(x + 1/N) + x(1 - P_{1}^{-}) + T^{-}(x - 1/N) \right] + \left[1 - (1 - x)P_{1}^{-} - x(1 - P_{1}^{-}) \right]T^{-}(x) \right\}$$
(23)
$$T^{-}(x) = \frac{1}{N} + \left(1 - \frac{1}{\tau}\right) \left\{ \left[(1 - x)P_{1}^{-}T^{-}(x + 1/N) + x(1 - P_{1}^{-}) + x(1 - P_{1}^{-}) T^{-}(x - 1/N) \right] + \left[1 - (1 - x)P_{1}^{-} - x(1 - P_{1}^{-}) \right]T^{-}(x) \right\} \\ + \frac{1}{\tau} \left\{ \left[(1 - x)P_{1}^{+}T^{+}(x + 1/N) + x(1 - P_{1}^{+}) T^{+}(x - 1/N) \right] + \left[1 - (1 - x)P_{1}^{-} - x(1 - P_{1}^{+}) T^{+}(x - 1/N) \right] + \left[1 - (1 - x)P_{1}^{+} - x(1 - P_{1}^{+}) T^{+}(x) \right\}.$$

Defining $S(x) = (T^+(x) + T^-(x))/2$, $\Delta(x) = (T^+(x) - T^-(x))/2$, expanding $T(x \pm 1/N)$ in a Taylor series as above and expanding to second order in γ one finds:

$$\frac{2}{\delta x(1-x)}\Delta = \left(1 - \frac{2}{N\delta}\right) \left\{ \gamma \left(\frac{1}{2} - x\right) \frac{S''}{N} + \gamma S' + \left[1 + \gamma^2 \left(\frac{1}{2} - x\right)^2\right] \frac{\Delta''}{N} \right\}$$

$$+ \gamma^{2} \left(\frac{1}{2} - x\right) \Delta' \bigg\}$$

$$- \frac{1}{x(1-x)} = \gamma \left(\frac{1}{2} - x\right) \frac{\Delta''}{N} + \gamma \Delta' + \left[1 + \gamma^{2} \left(\frac{1}{2} - x\right)^{2}\right] \frac{S''}{N}$$

$$+ \gamma^{2} \left(\frac{1}{2} - x\right) S'.$$
(24)

Eqs. (24) may be discussed in two different limits. The first is the case where τ is $\mathcal{O}(1)$, i.e., when $\delta \sim 1/N$. Unlike the case without storage considered in Section 4, where under fast switching of the environment the stochasticity becomes essentially demographic, here in this limit the storage effect is very strong and the lifetime of the system, as we shall see, is exponential in N when $N \rightarrow \infty$. The other, more relevant, case is when δ is fixed as N grows (meaning that the persistence time of the environmental fluctuations is independent of the size of the community); in this limit the storage effect is weaker, and the persistence time scales like a positive power of N in the asymptotic limit.

5.1. Strong storage effect

To consider a strong effect case, let us assume $\tau = 2$. This implies that after an elementary timestep the environment switches with probability 1/2, so there is effectively no persistence of the environmental conditions. In this scenario $\delta = 2/N$, meaning that the r.h.s. of the first equation in (24) vanishes, so $\Delta = 0$ (Δ measures the difference between $T^+(x)$ and $T^-(x)$, and there is no such difference if the environmental conditions are uncorrelated). Eqs. (24) then reduce to

$$S'' + N\gamma^2 \left(\frac{1}{2} - x\right) S' = -\frac{N}{x(1-x)},$$
(25)

where the γ^2 term in the coefficient of *S''* was neglected with respect to unity, since we assumed that γ is small. Eq. (25) is an inhomogeneous, first order equation for $W \equiv S'$; using an integrating factor to solve it, plugging in the boundary condition W(1/2) = 0 (meaning that the maximum lifetime of the system occurs at x = 1/2 since the two species are symmetric) and integrating again, one finds,

$$S(x) = -N \int_0^x dt \ e^{-N\gamma^2 t(1-t)/2} \int_t^{1/2} dq \frac{e^{N\gamma^2 q(1-q)/2}}{q(1-q)},$$
(26)



Fig. 3. Maximum persistence time, S(1/2), as a function of $g \equiv N\gamma^2/2$, for different values of N ($N = 2^n \cdot 10$ for n = 1..9) and $\gamma = 0.3$. Blue circles are the result obtained from a numerical solution of the BKE, red line is the large g asymptotic expression (27) and dashed green line shows the N log(2), demographic stochasticity relationship. The inset shows the same data on a double logarithmic scale, emphasizing the breakdown of (27) and the demographic noise behavior at small values of g.

where the boundary condition S(0) = 0 determines the lower bound of the outer integral.

As long as the quantity $g \equiv N\gamma^2/2$ is large, the main contribution to the inner integral comes from the peak close to 1/2 (the 1/a divergence when a approaches zero is regularized by the outer integral). The Laplace method then yields for the inner integral in the large g limit,

$$\int_t^{1/2} dq \frac{e^{N\gamma^2 q(1-q)/2}}{q(1-q)} \sim 2e^{g/4} \sqrt{\frac{\pi}{g-4}}.$$

The outer integration in the large g limit is trivial, since only the low t region contributes and one may replace t(1 - t) by t and extend the limits of integration to infinity. Accordingly,

$$S(1/2) \sim \frac{1}{\gamma^2} \sqrt{\frac{8\pi}{N\gamma^2 - 8}} e^{N\gamma^2/8}.$$
 (27)

As suggested by the denominator of the square root, this expression is valid only for $g \gg 4$. In the small g regime the logarithmic divergence close to zero dominates the inner integral and the problem converges to its demographic noise limit, as demonstrated in Fig. 3.

5.2. Weak storage effect

Now let us consider the case where δ is fixed while $N \to \infty$, so that the $2/(N\delta)$ in the upper line of Eq. (24) is negligible, meaning that we are dealing with the more realistic situation where δ , the correlation time of the environment, is fixed in units of a generation and is independent of the community size.

As in the case without the storage effect, it turns out that only the S' and the Δ term are important in the first equation of (24), and the Δ'' is negligible in both equations. This numerical observation may be justified, as before, as long as $\gamma^2 \delta$ and $\gamma^2 \delta^2$ are much smaller than one. Accordingly, Eqs. (24) reduce to,

$$\frac{2}{\delta x(1-x)}\Delta = \gamma S'$$

$$-\frac{1}{x(1-x)} = \gamma \Delta' + \frac{S''}{N} + \gamma^2 \left(\frac{1}{2} - x\right) S',$$
(28)

where we also omitted the γ^2 term in the coefficient of S'', since it is small compared to one.

The upper line of (28) implies $\gamma \Delta'(x) = \gamma^2 \delta \left[x(1-x)S''/2 + \right]$ (1/2 - x)S']. Plugging that into the second equation one finds,

$$\gamma^2 N(1+\delta) \left(\frac{1}{2} - x\right) S' + \left(1 + \frac{N\gamma^2 \delta x(1-x)}{2}\right) S''$$
$$= -\frac{N}{x(1-x)},$$
(29)

or, with $W \equiv S'$ and $F_1(x) \equiv 1 + N\gamma^2 \delta x (1-x)/2$,

$$W'(x)F_1(x) + W(x)F'_1(x)\frac{1+\delta}{\delta} = -\frac{N}{x(1-x)}.$$
(30)

Multiplying both sides of (30) by the integrating factor $F_1^{1/\delta}$ one may write (30) as

$$\frac{d}{dx}\left(W(x)F_1^{1+1/\delta}(x)\right) = -N\frac{F_1^{1/\delta}(x)}{x(1-x)}.$$
(31)

One integration over x yields W, where (by symmetry) the limits of integration are such that W(1/2) = 0. Accordingly,

$$S(x) = N \int_{0}^{x} dt F_{1}^{-1-1/\delta}(t) \int_{t}^{1/2} dq \frac{F_{1}^{1/\delta}(q)}{q(1-q)}$$
(32)
= $N \int_{0}^{x} dt (1 + Gt(1-t))^{-1-1/\delta} \int_{t}^{1/2} dq \frac{(1 + Gq(1-q))^{1/\delta}}{q(1-q)},$
with $C = N w^{2} \delta / 2$. Fig. 4 shows the correspondent between (22) and

with $G \equiv N\gamma^2 \delta/2$. Fig. 4 shows the agreement between (32) and the numerics.

Let us try to extract the large N asymptotic behavior of the maximum persistence time S(1/2). In the inner integral of (32) the integrand grows exponentially with *q* [for small *q* the numerator grows like $exp(Gq/\delta)$] so the main contribution comes from the regime $q > \delta/G$. As before, although the denominator contribution diverges logarithmically when the lower limit of the integral approaches zero (reflecting the effect of demographic stochasticity), this divergence is G-independent and is regularized by the outer integral. This observation allows us to factor the numerator of the inner integral,

$$\int_{t}^{1/2} dq \frac{(1+Gq(1-q))^{1/\delta}}{q(1-q)}$$

= $G^{1/\delta} \int_{t}^{1/2} dq [q(1-q)]^{-1+1/\delta} \left(1 + \frac{1}{Gq(1-q)}\right)^{1/\delta}$
 $\sim G^{1/\delta} \left(1 + \frac{4}{G}\right)^{1/\delta} \int_{t}^{1/2} dq [q(1-q)]^{-1+1/\delta}$ (33)

. ...

where in the last step we replaced the 1/q(1-q) term in the last factor by its value at q = 1/2, the region from which the main contribution comes (the same result may be obtained by Laplace integration around the maximum point at q = 1/2). Accordingly,

$$S(x) = NG^{1/\delta} \left(1 + \frac{4}{G} \right)^{1/\delta} \int_0^x dt \frac{1}{\left[1 + Gt(1-t) \right]^{1+1/\delta}} \\ \times \left[B_{\frac{1}{2}} \left(\frac{1}{\delta}, \frac{1}{\delta} \right) - B_t \left(\frac{1}{\delta}, \frac{1}{\delta} \right) \right].$$
(34)

Here $B_z(a, b)$ is the incomplete Beta function.

The main contribution to the outer integral (34) is from the $t \rightarrow 0$ regime, so $1 - t \approx 1$. In this limit $B_t(\frac{1}{\delta}, \frac{1}{\delta}) \approx t^{1/\delta}$. Accordingly, the maximum persistence time as $N \rightarrow \infty$ is,

$$S(1/2) \sim NB_{\frac{1}{2}}(\frac{1}{\delta}, \frac{1}{\delta}) \left(1 + \frac{4}{G}\right)^{1/\delta} \delta G^{1/\delta - 1}$$
$$= \frac{2}{\gamma^2} B_{\frac{1}{2}}(\frac{1}{\delta}, \frac{1}{\delta}) \left(1 + \frac{8}{\gamma^2 \delta N}\right)^{1/\delta} \left(\frac{\gamma^2 \delta}{2}N\right)^{1/\delta}.$$
(35)



Fig. 4. In the left panel, a comparison between the results of a Monte-Carlo simulations, numerical solution of the BKE and the analytic results (i.e., numerical evaluation of (32)) for S(x), is presented. Results are shown for N = 200, $\gamma = 0.4$ and $\delta = 0.2$. The MC lifetimes were averaged over 250 000 runs. In the right panel we compare the maximum lifetime of the system, S(1/2), with the predictions of Eq. (32), testing, again, both the accuracy of this formula and the general scaling hypothesis. Three full black lines, corresponding to the outcomes of (32) for different values of δ (appearing next to each line), are presented along with the results obtained using numerical solutions of the BKE. For the two sets $\delta = 0.05$ and $\delta = 0.1$, the green squares are the numerical results with N = 1000 and γ varies between 0.01 and 0.2, and the red circles represent the results for $\gamma = 0.2$ and $N \in [50..100]$. For $\delta = 0.2$, green squares correspond to N = 400 and $\gamma \in [0.01..0.4]$ while the red circles are $\gamma = 0.4$ and $N \in [50..400]$. All lines converge to ln(2), the demographic noise limit, as *G* goes to zero. Open diamonds are the lifetimes obtained from Monte-Carlo simulation of the process for $\delta = 0.2 \gamma = 0.4 N \in [50, 100, 200, 400]$, where each realization was averaged over at least 100 000 runs.

This expression is a very good approximation to the exact expression (32) as long as *G* is large. The term $(1 + 4/G)^{1/\delta}$ behaves in the large *G* limit like $exp(4/\delta G)$ and converges to one, yielding the asymptotic power-law behavior

$$S(1/2) \sim N^{1/\delta} \tag{36}$$

predicted by Hidalgo et al. (2017). One sees, however, that this asymptotic behavior emerges only when $G\delta = N\gamma^2\delta^2/2 \gg 4$. The approximation suggested in Eq. (35) captures a much wider range, as demonstrated in Fig. 5.

When a single mutant is introduced into the system, the persistence time is obtained from the integral (34) with an upper limit at x = 1/N. The result is

$$S(1/N) = \frac{\gamma^2}{2} S(1/2)$$

= $B_{\frac{1}{2}}(\frac{1}{\delta}, \frac{1}{\delta}) \left(1 + \frac{8}{\gamma^2 \delta N}\right)^{1/\delta} \left(\frac{\gamma^2 \delta}{2} N\right)^{1/\delta}.$ (37)

Unlike the case with no storage, now the persistence time of a single mutant has the same $N^{1/\delta}$ scaling as the maximum persistence time. Accordingly, the threshold to clonal interference occurs at much smaller values of ν , of order $N^{-(1+1/\delta)}$.

6. Storage effect against selection

For a system exposed to external migration, or allowing for a constant rate of mutations or speciation events, a strictly neutral/symmetric model, where the species fitnesses are assumed to be exactly equal (either literally or after averaging over time) is quite implausible. One should expect that phenotypic differences lead to some value of average selective advantage of one of the species. Even mechanisms like emergent neutrality (Kessler and Shnerb, 2014; Vergnon et al., 2012) yield competitive communities with slight selective variations between species.

When there is no storage in the system, selection determines the large N limit of the persistence time, and the effect of environmental stochasticity becomes irrelevant. Without storage, stochasticity yields only a random walk in the log-abundance space (see Section 2D) and the constant directional bias wins against such a random movement in the long run. In Appendix C we



Fig. 5. Persistence time for a system with weak storage effect ($\delta = 0.2$, $\gamma = 0.5$) is shown against $N \in [50, ..., 4000]$ on a double logarithmic scale. Blue circles are numerical results obtained from the BKE, Red full line was obtained from numerical integration of (32) and the green dashed line is the approximation (35). As predicted, the slope approaches $1/\delta = 5$ in the asymptotic limit, but to reach this limit $4/G\delta$ should be smaller than one. This condition is fulfilled here around N = 800. The approximation (35) holds for a much wider regime.

present an analysis of this case: the model considered in Section 4 is superimposed on fixed selective bias and the large *N* result is indeed identical to the result of a model with selection and without environmental stochasticity, analyzed in Appendix B.

A much more interesting question emerges when the storage effect, which gives stability to the system, interferes with a fixed selective advantage of one species. This question has been considered by Chesson and Warner (Chesson and Warner, 1981) (see also Hatfield and Chesson, 1989) who concluded that population fluctuations converge on a stationary stochastic process with all densities positive if $\gamma^2 > 2\eta_0$, i.e., if the stochasticity is strong enough with respect to the strength of selection. Here we consider the same problem from the persistence time perspective. We will show that the maximum time to absorption is superlinear in *N* when the stability parameter presented in Chesson and Warner (1981), $2\eta_0/\gamma^2$, is smaller than $1 - \delta$.

To model this scenario we change the dynamics of $\ln(\rho)$ in Eq. (22): instead of jumping from $+\gamma$ to $-\gamma$, $\ln(\rho)$ jumps between $\eta_0 + \gamma$ and $\eta_0 - \gamma$, meaning that species 2 has a fixed selective advantage η_0 , superimposed on the environmental fluctuations of amplitude γ .

Plugging this definition of η and P_1 into Eq. (23), one finds, to the leading order in η_0 ,

$$\frac{2}{\delta x(1-x)} \Delta = \left(1 - \frac{2}{N\delta}\right) \left\{ \gamma \left(\frac{1}{2} - x\right) \frac{S''}{N} + \gamma S' + \left[1 + \gamma^2 \left(\frac{1}{2} - x\right)^2\right] \frac{\Delta''}{N} + \gamma^2 \left(\frac{1}{2} - x\right) \Delta' \right\}$$
(38)
$$- \frac{1}{N} = \gamma \left(\frac{1}{2} - x\right) \frac{\Delta''}{N} + \gamma \Delta' + \left[1 + \gamma^2 \left(\frac{1}{2} - x\right)^2\right]$$

$$-\frac{1}{x(1-x)} = \gamma \left(\frac{1}{2} - x\right) \frac{\Delta^{*}}{N} + \gamma \Delta^{'} + \left\lfloor 1 + \gamma^{2} \left(\frac{1}{2} - x\right) \right\rfloor$$
$$\times \frac{S^{''}}{N} + \left[\gamma^{2} \left(\frac{1}{2} - x\right) - \eta_{0}\right] S^{'}.$$

Note that η_0 appears only in the last term of the lower equation. As before, dominant balance analysis allows us to simplify these equations,

$$\frac{2}{\delta x(1-x)}\Delta = \gamma S'$$

$$-\frac{1}{x(1-x)} = \gamma \Delta' + \frac{S''}{N} + \left[\gamma^2 \left(\frac{1}{2} - x\right) - \eta_0\right]S'.$$
(39)

With the definitions $W \equiv S'$, $F_1(x) \equiv 1 + Gx(1 - x)$, $G \equiv N\gamma^2 \delta/2$,

$$W'(x)F_1(x) + W(x)\left(-\eta_0 N + F'_1(x)\frac{1+\delta}{\delta}\right) = -\frac{N}{x(1-x)}.$$
 (40)

This is a first order equation for W that may be solved with an integration factor; however, since the problem is no longer symmetric the point at which W vanishes is not at x = 1/2. Labeling this point x^* , the result for S, taking into account the boundary condition S(0) = 0, is,

$$S(x) = N \int_0^x dt \frac{e^{-z(t)}}{(1 + Gt(1 - t))^{1 + 1/\delta}} \\ \times \int_t^{x^*} dq \frac{e^{z(q)}(1 + Gq(1 - q))^{1/\delta}}{q(1 - q)},$$
(41)

with

$$z(x) \equiv -\mu \operatorname{atanh}\left((2x-1)\sqrt{\frac{G}{G+4}}\right),\tag{42}$$

where

$$\mu = \frac{2\eta_0 N}{\sqrt{G(G+4)}} \approx \frac{4\eta_0}{\gamma^2 \delta},\tag{43}$$

the last approximation holding for large G.

To proceed, we first need to determine x^* , using the second boundary condition, S(1) = 0. Solving numerically for x^* , S(x) may be plotted against the numerical solutions of the BKE and the fit is very nice (Fig. 6).

To obtain the large *N* behavior of $S(x^*)$ from (41), we assume, as in the former section, that the main contribution of the inner integral comes from finite values of *q* (again, although the integrand blows up like 1/q at zero, this contribution is only logarithmic and is regularized by the outer integration). Expressing the hyperbolic tangent in terms of logarithms, the inner integral may be written



Fig. 6. Persistence time for a system with storage effect ($\delta = 0.1$, $\gamma = 0.2$, N = 1000) and selection $\eta_0 = 5 \cdot 10^{-3}$. The result obtained from numerical solution of the master equation (filled red circles) and those obtained from a numerical integration of (41) with G = 2 (dashed green line) are shown. The value $x^* = 0.723$ was obtained numerically from the condition S(1) = 0. As explained in the text, positive η_0 gives an average selective advantage to species 2, hence the lifetime of the system peaked to the right of x = 1/2.

as,

$$\begin{split} &\int_{t}^{x^{*}} dq \frac{e^{z(q)}(1+Gq(1-q))^{1/\delta}}{q(1-q)} = \tag{44} \\ &G^{1/\delta} \int_{t}^{x^{*}} dq \frac{[q(1-q)]^{1/\delta}}{q(1-q)} \left(\frac{q}{1-q}\right)^{-\mu/2} \left(1+\frac{1}{Gq(1-q)}\right)^{1/\delta} \\ &\times \left(\frac{\left(1+(2q-1)\sqrt{\frac{G}{G+4}}\right)(1-q)}{\left(1-(2q-1)\sqrt{\frac{G}{G+4}}\right)q}\right)^{-\mu/2}. \end{split}$$

Notice that the last two terms under the integral approach unity in the large G limit. Accordingly, we use for the Laplace integration of (44) only the terms that are important when G is large,

$$\int_{0}^{x^{*}} dq \ q^{\alpha} (1-q)^{\beta}.$$
(45)

The maximum of the integrand in (45) occurs at $\bar{q} = \alpha/(\alpha + \beta)$, where $\alpha = -1 + 1/\delta - \mu/2$ and $\beta = -1 + 1/\delta + \mu/2$ (we assumed $\alpha > 0$, see below). Note that, for positive values of μ , the maximum of *S*, *x*^{*}, moves to the right of 1/2 (see Fig. 6) while the maximum of the integrand occurs at $\bar{q} < 1/2$. This implies that (unless μ is very small, see below) the peak is within the range of integration.

Plugging $q = \overline{q}$ in the last two terms and using Laplace integration one obtains for the inner integral,

$$\left(1+\frac{1}{G\overline{q}(1-\overline{q})}\right)^{1/\delta} \left(\frac{\left(1+(2\overline{q}-1)\sqrt{\frac{G}{G+4}}\right)(1-\overline{q})}{\left(1-(2\overline{q}-1)\sqrt{\frac{G}{G+4}}\right)\overline{q}}\right)^{-\mu/2} \times \sqrt{\frac{2\pi\alpha\beta}{(\alpha+\beta)^3}} \,\overline{q}^{\alpha}(1-\overline{q})^{\beta}G^{1/\delta}.$$
(46)

To deal with the outer integral, one notices that the contribution of the outer integral comes mainly from the $t \ll 1/G$ region. In that case, z(t) should be expanded for small t and large G, such that Gtis fixed, yielding

$$z(t) \approx -\frac{\mu}{2}\ln(x+1/G). \tag{47}$$

Since the inner integral is now a constant, the contribution of the outer integral will be

$$\int_{0}^{x^{*}} dt \frac{e^{-z(t)}}{(1+Gt(1-t))^{1+1/\delta}} \approx G^{-\frac{\mu}{2}} \int_{0}^{\infty} \frac{dt}{(1+Gt)^{-1+\mu/2-1/\delta}} \approx \frac{G^{-\frac{\mu}{2}}}{G(1+1/\delta-\mu/2)}.$$
 (48)

The final form of the large N approximation is (the absolute value signs will soon be justified), is,

$$S(x^*) \sim \left(1 + \frac{1}{G\overline{q}(1-\overline{q})}\right)^{1/\delta} \\ \times \left(\frac{\left(1 + (2\overline{q}-1)\sqrt{\frac{G}{G+4}}\right)(1-\overline{q})}{\left(1 - (2\overline{q}-1)\sqrt{\frac{G}{G+4}}\right)\overline{q}}\right)^{-\mu/2} \\ \times \sqrt{\frac{2\pi\alpha\beta}{(\alpha+\beta)^3}} \frac{2\overline{q}^{\alpha}(1-\overline{q})^{\beta}}{\gamma^2\delta(1+1/\delta-|\mu|/2)} G^{\frac{1-|\overline{\delta}|}{\delta}}.$$
(49)

Here we define the dimensionless selection parameter mentioned above,

$$\tilde{s} \equiv \frac{2\eta_0}{\gamma^2},$$

this parameter measuring the strength of the selection in units of the environmental stochasticity.

The terms in the first two parentheses of (49) approach unity at large *G*, but are important when *G* is small. When all other parameters are kept fixed and *N* increases the lifetime of the community grows like,

$$S(x^*) \sim N^{\frac{1-|S|}{\delta}}.$$
(50)

All these features are demonstrated in Fig. 7. Comparing (50) with (35), one notices that the main effect of selection in the large *N* limit is to decrease the exponent of *N*, from $1/\delta$ to $(1 - |\tilde{s}|)/\delta$. Our approximation, as we noted right after Eq. (45), is based on the assumption $\alpha > 0$, which is translated to the condition that the growth of $S(x^*)$ with *N* is superlinear. We did not calculate the lifetime of the system in the $\tilde{s} > 1 - \delta$ regime, but clearly when $\tilde{s} \rightarrow \infty$ the *N* scaling has to be logarithmic (see Appendix B).

Until now we have assumed that the values of η_0 , μ and \tilde{s} are all positive, but in Eqs. (49) and (50) we take the absolute values of these quantities in the last terms. The reason for that is as follows. When η_0 is negative x^* occurs to the left of 1/2, while $\bar{q} > 1/2$. The inner integration may be done using Laplace integrals only if the peak is inside the integration region, i.e., it should include the region between x^* and x = 1, meaning that the outer integral has to be done over the range between x and 1. The main contribution to the outer integral in this range comes from values of t around one, so the sign of μ in the expression for z(t) is inverted. Accordingly, the quantities that depend on μ from the outer integral appear with an absolute value sign. The μ in the second parentheses of (49) comes from the inner integration and do not change sign, but since $\bar{q}(\eta_0) = 1 - \bar{q}(-\eta_0)$, the result is the same.

The discussion that leads to Eq. (49) was based on the assumption that the inner integration region contains most of the Gaussian peak around \bar{q} . This is not exactly true when $1/\mu$ and δ are not small, as both \bar{q} and x^* approach 1/2, and in the extreme limit $\mu = 0$ only half of the peak is integrated, meaning that (49) should be multiplied by 1/2. In general one needs to multiply (49) by $(1 + \text{Erfc} [(x^* - \bar{q})/\sigma])/2$, where $\sigma = \sqrt{\alpha\beta/(\alpha + \beta)^3}$.



Fig. 7. Log of the maximum persistence time, $S(x^*)$, is plotted versus $\ln(N)$ for a system with storage effect ($\delta = 0.1$, $\gamma = 0.2$) and selection. Orange circles correspond to $\eta_0 = \tilde{s} = 0$, green diamonds represent $\eta_0 = 0.005$, $\tilde{s} = 1/4$, purple hexagrams are for $\eta_0 = 0.01$, $\tilde{s} = 1/2$ and the brown squares are $\eta_0 = 0.02$, $\tilde{s} = 1$. The data obtained from numerical integration of Eq. (41) and the full lines are the large *N* approximation (49) for each case.

7. Discussion

Coexistence of many competing species in a local community and the maintenance of multiple alleles in a gene pool are ubiquitous in natural systems. Standard explanations to these phenomena, like strong niche differentiation (in ecology) or heterozygote advantage (in population genetics), are subject to some theoretical challenges, at least in the case of high-diversity assemblages. For example, May (May, 1972) pointed out that if the niche overlap between species is substantial the chance of a system of many species to admit a stable equilibrium decreases exponentially with the number of species. Therefore, the search for alternative coexistence mechanisms became a subject of intensive research (Chesson, 2000).

The (temporal) storage effect, suggested by Chesson and coworkers, is apparently an appealing candidate. Environmental stochasticity is almost always quite strong in biosystems (see, e.g. Hekstra and Leibler (2012), where fluctuations scale with abundance, and not with the square root of the abundance, even under extremely stable external conditions. See also Kalyuzhny et al., 2014b; Kalyuzhny et al., 2014a; Chisholm et al., 2014 for an analysis of "standard" high diversity ecosystems, showing that the main driver is environmental stochasticity). Accordingly, the fact that it may become a stabilizing factor, supporting the growth of rare species and providing an effective frequency dependent selective mechanism, is very interesting.

From a different perspective, the ubiquitous presence of environmental stochasticity leads to attempts to incorporate it into the neutral model—one of the main theoretical frameworks in both population genetics and community ecology (Chisholm et al., 2014; Kalyuzhny et al., 2014b, 2015; Danino et al., 2016). Biodiversity under neutral dynamics relays on speciation–absorption equilibrium, and as we have seen here, environmental stochasticity affects strongly the absorption rates. The works published so far have relied on a mix of numerical experiments and a few analytic arguments. A general theoretical understanding of the time averaged neutral model, comparable with classical results that were obtained for the neutral model with demographic stochasticity (like the Fisher log-series and zero-sum multinomials), is still missing.

Herein we have extended the results of Hidalgo et al. (2017) and discussed a few models that incorporate environmental stochasticity, selection and demographic noise, for a two species community. These results are of interest in and of themselves, as they provide a new insight to the classical works of Chesson and Warner (1981), Hatfield and Chesson (1989) and Hatfield and Chesson (1997), shedding light on the question of a community's persistence time. Moreover, our results provide an answer to a fundamental question: at what rate one should introduce new types to the system in order to maintain it in a diverse state.

There are still many open questions, including the behavior of higher moments of the persistence time for the model with storage (without storage, or with pure demographic stochasticity, the variance of the persistence time is equal to the time itself, as one can understand from the Galton–Watson theory or from the theory of first passage time, correspondingly). The problem of the fixation time (which is assumed to determine the pace of the evolutionary process) is also of interest.

However, we believe that the most important aspect of the work presented here is as a first step towards an analytic theory of neutral dynamics with environmental stochasticity. Generalization of our work from the two species case to a many species community will allow one to find the species abundance distributions and the species richness for the time averaged neutral theory of biodiversity in stable mutation–extinction equilibrium, and even to incorporate weak effects of selection into the otherwise symmetric model (as we did numerically in Danino et al. (2016)). We intend to address these topics in subsequent publications.

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Appendix A. Methods

Throughout this work we compare the analytic results, obtained from the backward Kolmogorov equations (BKE), to the results obtained from three types of numerics: agent-based Monte-Carlo simulation of the birth-death process, numerical solutions of the BKE itself and numerical integrations of expressions like (41).

A.1. Monte-Carlo simulations

The agent based simulations were performed as follows. We start with a community of *N* individuals, in which *xN* belong to species #1 and N(1 - x) belong to species #2.

To simulate neutral dynamics with pure demographic stochasticity (Section 3), two individuals are chosen at random in each elementary step, with probability 1/2 the first dies and is replaced by an offspring of the second (meaning that after the replacement both individuals belong to the species of the second) and with probability 1/2 the second dies and is replaced by the offspring of the first. After each elementary step the time is incremented by 1/N. The persistence time of the community is defined as the mean time elapsed until one of the species goes extinct, and we measure it by running many histories with the same initial condition and averaging over the outcomes.

For the system with fixed selection, or with environmental stochasticity with no storage effect (Appendix B, Section 4), the same procedure is used, where now if two individuals belonging to different species are involved in a duel, the chance of each to win is determined by its relative fitness. The relative fitness is time independent in a fixed environment and fluctuates between the values $\eta_0 \pm \gamma$ in the case of environmental stochasticity.

The storage effect is considered in Section 5 and the interplay between the storage effect and the presence of overall selective advantage is considered in Section 6. In both cases the simulation procedure is different: in each elementary step one individual is chosen at random to die, and then the species that is recruited to fill the gap is determined according to the abundance weighted by the fitness, as set out in Eqs. (22).

A.2. Numerical solution of the backward Kolmogorov equation

The discrete BKEs considered through this paper, like Eqs. (11) and (23), are second order, linear, inhomogeneous difference equations that have the general form,



where $W_{n,m}$ is the rate of transitions from the *n* to the *m* state. Accordingly, the values of T_n^{\pm} [and consequently the values of S(n) and $\Delta(n)$] may be determined by inverting this $2N - 2 \times 2N - 2$ matrix and multiplying the outcome by the constant vector -1/N.

Appendix B. Pure selection without environmental stochasticity

In this appendix we calculate the persistence time of a mutant species of fitness η_0 with *n* individuals in a two species community of size *N* under fixed selective pressure (no environmental fluctuations) with demographic stochasticity.

The model is the same model considered in Section 4 for environmental stochasticity with no storage effect; each elementary step two individuals are chosen at random for a duel. If they belong to the same species nothing happens, if they belong to different species then species #1 wins with probability q and species #2 wins with probability 1 - q. The loser dies and an offspring of the winner takes its slot, so $n \rightarrow n \pm 1$. The environment is fixed, meaning that $q = 1/2 - \eta_0$. When $\eta_0 \rightarrow 0$, the result should converge to (6), while if the effect of selection is strong one expects the asymptotic $log(N)/\eta_0$ dependency.

The BKE may be derived from (11) by taking $\tau \to \infty$,

$$T_n = \frac{1}{N} + F_n \left[q T_{n+1} + (1-q) T_{n-1} \right] + \left[1 - F_n \right] T_n.$$
(B.1)

Moving to the continuum limit (as before F = 2x(1 - x) where x = n/N), expanding *T* in a Taylor series and keeping derivatives up to the second order one obtains,

$$T'' + \eta_0 N T' = -\frac{N}{x(1-x)},$$
(B.2)

The solution to this equation is immediate. Using an integrating factor we get

$$(T' \exp(\eta_0 N x))' = -N \exp(\eta_0 N x)/(x(1-x)),$$

and this vields.

$$T(x) = N \int_0^x dt e^{-\eta_0 N t} \int_t^{x^*} dq \frac{\exp(\eta_0 N q)}{q(1-q)},$$
(B.3)

where x^* is determined by the condition T(1) = 0 (see Section 6). If $\eta_0 = 0$, $x^* = 1/2$ and the integrals yield the demographic noise result $T(x) = -N[x \log(x) + (1 - x) \log(1 - x)]$, as expected.

The integrals (B.3) are doable even for finite η_0 , yielding a result in terms of hyperbolic arctangents and exponential integrals. To find x^* using the condition T(1) = 0 we used this analytic solution, plugged in the limits at zero and one, expanded the result for large $\eta_0 N$ and solved for x^* to find,

$$x^* \sim \frac{\ln \ln(\eta_0 N)}{n_0 N}.\tag{B.4}$$

Since x^* is small in the large N limit, the (1 - q) term in the denominator of the inner integral may be neglected if one looks for the maximum persistence time. The leading term for this quantity is,

$$T(x^*) \sim \frac{2\ln(\eta_0 N)}{\eta_0}.$$
 (B.5)

Appendix C. Selection and environmental stochasticity without storage

Here we consider the effect of a time independent selective advantage of species #1, when superimposed on environmental stochasticity, without storage. Practically we are looking at the model considered in Section 4, when the chance of species 1, say, to win a duel jumps between $1/2 + \eta_0/4 + \gamma/4$ and $1/2 + \eta_0/4 - \gamma/4$, so η_0 is the time independent component of the fitness. Since we have no storage the dynamics resembles that of a random walker (in log abundance space) with fixed bias towards one of the edges, so when *N* goes to infinity one expects that $S_{max} \sim \ln(N)/\eta_0$, while for small *Ns* and weak η_0 the $\ln^2(N)$ behavior found in Section 4 dominates.

The BKE (with $q_1 \equiv 1/2 + \gamma/4 + \eta_0/4$ (q_1 is the chance to jump to the right in the plus phase) and $q_2 \equiv 1/2 + \gamma/4 - \eta_0/4$) (q_2 is the chance to jump to the left in the minus phase) reads,

$$T_{n}^{+} = \frac{1}{N} + \left(1 - \frac{1}{\tau}\right) \left\{ F_{n} \left[q_{1} T_{n+1}^{+} + (1 - q_{1}) T_{n-1}^{+} \right] + [1 - F_{n}] T_{n}^{+} \right\} \\ + \frac{1}{\tau} \left\{ F_{n} \left[q_{2} T_{n-1}^{-} + (1 - q_{2}) T_{n+1}^{-} \right] + [1 - F_{n}] T_{n}^{-} \right\}$$
(C.1)

$$T_n^- = \frac{1}{N} + \left(1 - \frac{1}{\tau}\right) \left\{ F_n \left[q_2 T_{n-1}^- + (1 - q_2) T_{n+1}^- \right] + [1 - F_n] T_n^- \right\} \\ + \frac{1}{\tau} \left\{ F_n \left[q_1 T_{n+1}^+ + (1 - q_1) T_{n-1}^+ \right] + [1 - F_n] T_n^+ \right\}.$$

Defining $S_n = (T_n^+ + T_n^-)/2$, $\Delta_n = (T_n^+ - T_n^-)/2$, moving to the continuum limit and expanding $T(x \pm 1/N)$ to second order in 1/N above, one finds:

$$\frac{2\Delta}{\tau x(1-x)} = \left(1 - \frac{2}{\tau}\right) \left[\frac{\gamma}{N}S' + \frac{\Delta''}{N^2} + \eta_0\frac{\Delta'}{N}\right]$$

$$-\frac{1}{x(1-x)} = \frac{S''}{N} + \gamma \Delta' + \eta_0 S'.$$
(C.2)

For small δ this yields (see Section 4),

$$\frac{2\Delta}{\delta x(1-x)} = \gamma S' + \frac{\Delta''}{N} + \eta_0 \Delta'$$

$$-\frac{1}{x(1-x)} = \frac{S''}{N} + \gamma \Delta' + \eta_0 S'.$$
(C.3)

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

$$-\frac{N}{x(1-x)} = [1 + Gx(1-x)]S'' + [\eta_0 N + G(1-2x)]S'.$$
(C.4)



Fig. 8. Maximum persistence time, $S(x^*)/N$, is plotted versus *x* for a system with no storage effect ($\delta = 0.1$, $\gamma = 0.1$, N = 1000) and selection ($\eta_0 = 0.01$). Red circles were obtained from numerical solution of the integrals (C.5), where the value of x^* was found from the condition S(1) = 0. The full blue line was obtained from the numerical solution of the BKE with the same parameters.

Solving this equation using an integrating factor, the expression for *S* is,

$$S(x) = N \int_{0}^{x} dt \frac{\left(\frac{1-2t-\sqrt{1+4/G}}{1-2t+\sqrt{1+4/G}}\right)^{-\mu/2}}{1+Gt(1-t)} \\ \times \int_{t}^{x^{*}} dq \frac{\left(\frac{1-2q-\sqrt{1+4/G}}{1-2q+\sqrt{1+4/G}}\right)^{\mu/2}}{q(1-q)},$$
(C.5)

where $G = N\gamma^2 \delta/2$ is the same parameter used in Section 4, x^* is the value of x where S reaches its maximum and

 $2\eta_0 N$

$$\mu \equiv \frac{2\eta_0 N}{\sqrt{G(G+4)}}.$$
 (C.6)

When $G \rightarrow 0$ Eq. (C.4) converges to (B.2) for a system with demographic stochasticity and selection but without environmental stochasticity, while if $\eta_0 \rightarrow 0$ we recover Eq. (13). μ reflects the relative strength of selection in comparison with the environmental stochasticity; for large *G*,

$$\mu \rightarrow 4\eta_0/(\gamma^2 \delta).$$

Fig. 8 shows the fit between the numerical solution of the BKE and the results obtained from a numerical solution of the integral (C.5).

To illustrate how selection dominates the behavior when $N \rightarrow \infty$, one note that in this limit $\sqrt{(4+G)/G} \sim 1 + 2/G$, so (C.5) may be written as,

$$S(x) = N \int_0^x dt \, \frac{\left(\frac{1-t}{1+Gt}\right)^{\mu/2}}{1+Gt(1-t)} \int_t^{x^*} dq \, \frac{(1+Gq)^{\mu/2}}{q(1-q)^{1+\mu/2}}.$$
 (C.7)

Let us assume, for the moment, that while x^* approaches zero when N is large, $Gx^* \gg 1$ in this limit. In such a case the 1 + Gq may be replaced by Gq in the numerator of the inner integral of (C.7), since the main contribution is from the upper bound. The inner integral is then solvable, and the contribution from the outer integral may be evaluated by calculating it in three different regimes: for $0 < t < \zeta$ ($\zeta \ll 1$, $G\zeta \gg 1$), $1 - \epsilon < t < 1$ (again ($\epsilon \ll 1$, $G\epsilon \gg 1$) and $\zeta < t < 1 - \epsilon$ and using asymptotic matching. To satisfy S(1) = 0 one finds that x^* must fulfill,

$$\left(\frac{x^*}{1-x^*}\right)^{\mu/2} \frac{1}{\mu G} = \frac{\ln(G)}{G^{1+\mu/2}},\tag{C.8}$$

i.e. (assuming, again, $x^* \ll 1$),

$$(x^*)^{\mu/2} \sim \mu \frac{\ln(G)}{G^{\mu/2}}.$$

Note that the assumption $Gx^* \gg 1$ turns out to be self consistent. Evaluating the outer integral of (C.7) from zero to x^* yields the community persistence time as $N \to \infty$,

$$S(x^*) \sim \frac{2\ln(\eta_0 N)}{\eta_0} \tag{C.9}$$

as obtained in Appendix B for selection without demographic stochasticity [Eq. (B.5)].

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