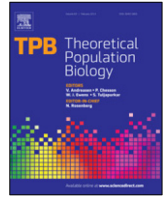




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Stability of two-species communities: Drift, environmental stochasticity, storage effect and selection

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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 drive 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 persistence time of 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 mechanism 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

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 rate in which the system jumps from one state to another, 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 two-species 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 was occurred, in their work, when the fraction of a 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 sub-leading terms in this asymptotic series. This allows us to identify the parameter region where the asymptotic 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 differences 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 along this paper, introduce the notations, provide a glossary (see Table 1) and briefly sketch the main results.

Throughout this paper we consider a 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.

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