



Species coexistence in a neutral dynamics with environmental noise



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ABSTRACT

Environmental fluctuations have important consequences in the organization of ecological communities, and understanding how such a variability influences the biodiversity of an ecosystem is a major question in ecology. In this paper, we analyze the case of two species competing for the resources within the framework of the neutral theory in the presence of environmental noise, devoting special attention on how such a variability modulates species fitness. The environment is dichotomous and stochastically alternates between periods favoring one of the species while disfavoring the other one, preserving neutrality on the long term. We study two different scenarios: in the first one species fitness varies linearly with the environment, and in the second one the effective fitness is re-scaled by the total fitness of the individuals competing for the same resource. We find that, in the former case environmental fluctuations always reduce the time of species coexistence, whereas such a time can be enhanced or reduced in the latter case, depending on the correlation time of the environment. This phenomenon can be understood as a direct consequence of Chesson's storage effect.

1. Introduction

One of the main problems in theoretical biology relies on the search for mechanisms leading to the conservation of biodiversity (Hooper et al., 2005). Looking at natural systems, it still remains unclear how some ecosystems are able to maintain such a large variety of species (McCann, 2000), such as in tropical forests (Volkov et al., 2005), phytoplankton in oceans (De Vargas et al., 2015), and coral reefs (Sale, 1977), to name but a few. More generally, explaining the stability of large complex ecological networks remains an open and debated issue (Montoya et al., 2006; Allesina and Tang, 2012; Suweis et al., 2014) and many works have proposed different mechanism as possible contributors in the maintenance of biodiversity in both trophic (Johnson et al., 2014; Allesina et al., 2015) and mutualistic (Bascompte and Jordano, 2007; Suweis et al., 2015) communities.

Abiotic conditions such as the temperature, light, precipitations, humidity, available nutrients in soil, etc., strongly influence the organization and biodiversity of ecological systems (Dunson and Travis, 1991). Furthermore, immutable environments could be considered an oddity in Nature (Pearman et al., 2008). Many theoretical studies have tried to explain the impact of environmental fluctuations on population growth and ecosystem stability (Lewontin and Cohen, 1969; Melbinger and Vergassola, 2015; May, 1973; Chevin et al., 2010) and its influence on evolutionary dynamics (Levins, 1968; Frank and Slatkin, 1990; Ashcroft et al., 2014); others have analyzed the role of environmental changes in prey-predator dynamics (Luo and Mao,

2007; Zhu and Yin, 2009; Dobramysl and Täuber, 2013), dispersal (McPeck and Holt, 1992; Yoshimura and Jansen, 1996) and the development of survival mechanisms to deal with unpredictable environments, usually referred to as bet-hedging strategies (Kussell and Leibler, 2005).

The question about how biodiversity can be maintained have been also addressed within the framework of the Neutral Theory of Biodiversity (NTB) (Hubbell, 2001; Azaele et al., 2016). This paradigm establishes a perfect equivalence among individuals, and, despite being a simple theory, has been able to describe and understood many ecological patterns observed in Nature (Hubbell, 2001; Azaele et al., 2016). Only recently, some works have studied the impact of environmental noise in neutral dynamics (Kessler and Shnerb, 2014; Kalyuzhny et al., 2015; Kessler et al., 2015; Melbinger and Vergassola, 2015). For instance, it has been argued that, although the NTB leads to successful predictions for static patterns, the theory fails to estimate several dynamical measures (Kalyuzhny et al., 2015), such as the scaling of species abundance fluctuations with the total population size. Environmental noise seems to fix these issues while preserving the previously reported phenomenology for the static patterns (Kessler and Shnerb, 2014; Kalyuzhny et al., 2015; Kessler et al., 2015).

Nevertheless, the role of environmental variability in maintaining the biodiversity of communities of neutral species is an open question. Indeed, it still needs to be clarified whether environmental noise has a positive or negative impact on species coexistence. For instance the

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authors of reference (Melbinger and Vergassola, 2015) study the dynamics of bacterial communities growing under limited conditions that respond differently to environmental fluctuations but are neutral on average. They show that environmental noise always reduces the possibility of species to coexist. In contrast, in another recent work (Danino et al., 2016), authors analyze the impact of the environment in a time-average neutral metacommunity model, showing that, under certain conditions, the total number of species supported by the ecosystem increases due to the variability of the environment. This can be viewed as a direct consequence the so-called *storage effect* evidenced by Chesson and Warner (1981). Furthermore, it has been reported that, in order to obtain such a mechanism, it is crucial that environmental stochasticity affects recruitment instead of mortality rates (Chesson and Warner, 1981; Kalyuzhny et al., 2015). However, a deep understanding of this issue from a theoretical point of view is still missing.

The goal of this paper is to shed some light on this variety of phenomenologies. To this end, we focus on the simple scenario in which two species compete for the resources with the dynamics of the voter-model (Castellano et al., 2009) in a well-mixed situation (i.e. neglecting spatial effects), with the key ingredient that the rates at which species colonize new sites vary with the environment. The model constitutes a general framework in which different dynamics (e.g. environmental variability affecting species mortality instead of recruitment rates, etc.) are mapped into different functional dependencies of the model parameters on the environmental variables. For each scenario, we compute analytically and numerically the mean time of coexistence before one of the species monodominates in the community, and we show that such a time can be enhanced or reduced by the effect of the environment depending on the specific case and on the characteristic time correlation of the environment. We provide a general model that helps clarify what is the net effect of the environment in neutral communities, but the specific dynamics has to be chosen depending on the particularities of the real system under consideration.

2. Voter model with environmental noise

The voter model was first formulated in the context of social dynamics to study how different opinions “compete” in a social network until, eventually, a general consensus is reached (Castellano et al., 2009). Different variants have been devised to analyze ecological problems with great success, in particular the voter model with speciation (Azaele et al., 2016) of the Neutral Theory of Biodiversity to which we have already referred.

Here we analyze the simple case of two competing species without speciation nor migration, and consider a fixed population of N individuals that can be either of species A or B . For the generalization of the model with environmental variability, it is convenient to introduce different fitnesses λ_A and λ_B for species A and B , respectively. We restrict our analysis to the case of a well-mixed community (i.e. mean-field) in which the spatial organization of the community is not considered.

In the dynamics, one individual is randomly chosen at each time step with uniform probability, removed from the population and replaced by a copy of one of its neighbors (in our case any individual in the community) with a probability proportional to its fitness. This process can be mapped into the following set of “chemical reactions”:



Let us note that the previous formulation is also valid for a dynamics with asymmetric mortality and equal recruitment rates, i.e. when the probability of removing an individual of species A (B) is not uniform but proportional to its mortality rate d_A (d_B), and the vacant place is

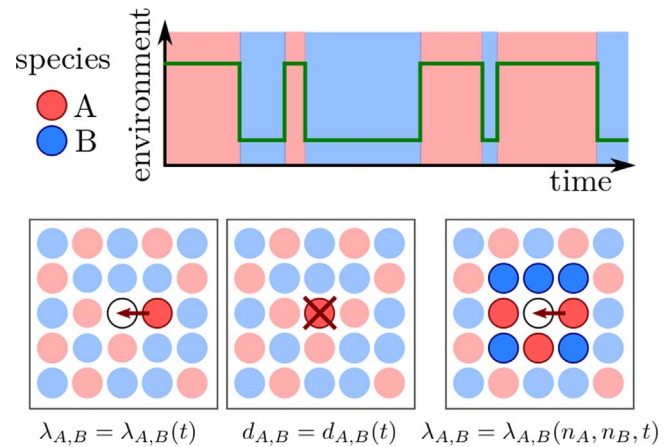


Fig. 1. A community of individuals of two species, A and B (identified with colors red and blue, respectively), competing for the available resources in a lattice (sites) with the dynamics of the voter model. (Top panel) Environment changes in time, alternating between periods that favors one of the species (corresponding shaded region) while disfavors the other one. We distinguish several cases depending on how the environment modulates mortality and/or recruitment rates: (Bottom Left Panel) An individual of species A (resp. B) occupies one of its adjacent places at rate $\lambda_A(t)$ (resp. $\lambda_B(t)$), independently of its surrounding neighbors. (Bottom Central Panel) Equivalently, an individual of species A (similarly for B) is killed at rate $d_A(t)$ (resp. $d_B(t)$), and then replaced by a random neighbor with uniform probability. For these two cases, species fitness does not depend on the local species density. In contrast, in (Bottom Right Panel), an individual of species A (and similarly for B) colonizes one if its adjacent sites, but the colonization rate is re-scaled by the total local fitness. This leads to a more complicated situation in which recruitment depends on the number of neighbors of species A and B , that we call n_A and n_B , respectively, so that $\lambda_A = \lambda_A(n_A, n_B, t)$.

occupied by a copy of a random neighbor with uniform probability. In such a case, Eq. (1) still holds if we replace $\lambda_{A,B} \rightarrow d_{B,A}$.

In a neutral scenario, species fitnesses are constant and equal, $\lambda_A = \lambda_B$, and species abundance in the population changes only due to demographic fluctuations. Eventually, one of the species can monodominates and the dynamics stops. It is known that, for well-mixed populations, the time to reach such a monodominant state in the voter model scales linearly with the population size (Castellano et al., 2009). This constitutes our point of reference when analyzing the impact of environmental fluctuations on species coexistence.

We aim to model a situation in which species fitness depends on external, variable, conditions. We consider the simple case in which the state of the environment is encoded in a random variable, $\epsilon = \epsilon(t)$, that alternates between two possible states, $\epsilon(t) = \pm 1$, at constant rate k (as sketched in top panel of Fig. 1), i.e. the environment is described by a dichotomous Markov noise (DMN). The choice of DMN stems from several reasons: i) it allows for mathematical treatment (see Bena (2006)) for a review on the theory of DMN, ii) it has a finite correlation time, $\tau = (2k)^{-1}$ (Bena, 2006), and iii) fluctuations are bounded, in contrast with other colored noises such as the Ornstein-Uhlenbeck process (Gardiner, 1985). With this choice, species fitness in Eq. (1) becomes time dependent, $\lambda_{A,B} \rightarrow \lambda_{A,B}(t) = \lambda_{A,B}(\epsilon(t))$, and there is an additional reaction equation for the environmental variable:



Species fitnesses can differ from time to time, but neutrality among species is conserved *on average*, so that $\langle \lambda_A(t) \rangle = \langle \lambda_B(t) \rangle$, where $\langle \cdot \rangle$ refers to the temporal average.

In the well-mixed scenario, the state of the system is fully represented by the number of individuals of species A , n_A , and the state of the environment, ϵ . We can write the Master equation for the probability of finding the system in a state (n_A, ϵ) , and after performing a Kramers-Moyal expansion in terms of the species A density, $x = n_A/N$,

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