The effect of environmental stochasticity on species richness in neutral communities

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HIGHLIGHTS

- The recently proposed time-averaged neutral theory is analyzed.
- The effect of demographic stochasticity on the storage mechanism is examined.
- Unimodal effect of environmental stochasticity on species richness is explained.

ARTICLE INFO

ABSTRACT

Environmental stochasticity is known to be a destabilizing factor, increasing abundance fluctuations and extinction rates of populations. However, the stability of a community may benefit from the differential response of species to environmental variations due to the storage effect. This paper provides a systematic and comprehensive discussion of these two contradicting tendencies, using the metacommunity version of the recently proposed time-average neutral model of biodiversity which incorporates environmental stochasticity and demographic noise and allows for extinction and speciation. We show that the incorporation of demographic noise into the model is essential to its applicability, yielding realistic behavior of the system when fitness variations are relatively weak. The dependence of species richness on the strength of environmental stochasticity changes sign when the correlation time of the environmental variations increases. This transition marks the point at which the storage effect no longer succeeds in stabilizing the community.

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1. Introduction

One of the biggest puzzles in community ecology is the persistence of high-diversity assemblages. The competitive exclusion principle (Gause, 2003; Hardin et al., 1960) predicts that the number of species coexisting in a local community should be fewer than or equal to the number of limiting resources, in apparent contrast with the dozens and hundreds of locally coexisting species of freshwater plankton (Hutchinson, 1961; Stomp et al., 2011), trees in tropical forests (Ter Steege et al., 2013) and coral reef species (Connolly et al., 2014). This problem has received considerable attention in recent decades, with many mechanisms suggested to circumvent the mathematical constraints embodied in the exclusion principle and many works that try to provide empirical support to these theories (Chesson, 2000; Gravel et al.,

2011; Amarasekare, 2003).

Within this framework, neutral theories, and in particular the neutral theory of biodiversity (NTB) suggested by Hubbell (2001), Volkov et al. (2003), and Rosindell et al. (2011), play an important role. Under neutral dynamics all individuals are considered as having the same fitness, and abundance variations are the result of demographic noise alone. The number of individuals belonging to each species varies randomly within the limit imposed by the overall size of the community, with most populations eventually drifting to extinction. However, the neutral turnover rate is very slow, and diversity is maintained due to the introduction of new species into the system, either via speciation (in the metacommunity) or by migration (in a local community).

The slow turnover dynamics in the neutral model is not only an advantage, it is also a disadvantage, and has triggered one of the main lines of criticism directed at the neutral model. It turns out that pure ecological drift is far too slow to account for both the observed short-term fluctuations and the long term dynamics (Ricklefs, 2006; Nee, 2005; Leigh, 2007; Kalyuzhny et al., 2014a,

2014b; Chisholm et al., 2014). For example, the abundance of the most common species in the Barro-Colorado Island Smithsonian 50 ha plot has decreased from 40,000 to 30,000 individuals (>1 cm dbh) during about half of a generation, while under pure demographic noise one expects variations of order $\sqrt{N} \sim 200$ within a whole generation. The abundance of the most common species in the Amazon basin is about 10^9 individuals (Ter Steege et al., 2013). Under neutral dynamics, this is the expected age (in generations) of that species, and since the generation time for tropical trees is about 50 years, this timescale ($5 \cdot 10^{10}$ y) is longer than the age of the universe (Ricklefs, 2006; Nee, 2005; Leigh, 2007). Recent work (Chisholm and ODwyer, 2014; see also Danino and Shnerb, 2015) shows that species' ages in neutral models are in fact lower than these early estimates by about two orders of magnitude, however these ages are still too high to be realistic.

Motivated by these difficulties, recent works (Kalyuzhny et al., 2015; Kessler and Shnerb, 2014) have pointed towards a generalized neutral theory that will include both demographic and *environmental* stochasticity. Basically, this new model accepts the equivalence principle, but assumes that the fitness of all species, *when averaged over time*, are equal while at any instant some species have higher fitness than the others due to temporal variations in parameters such as temperature, precipitation, etc. Accordingly, all species are equivalent and abundance variations are driven by fluctuations (Azaele et al., 2016). The ability of this time-averaged neutral theory of biodiversity (TNTB) to explain various empirical patterns, including species abundance distributions, temporal fluctuations statistics and the growth in system dissimilarity over time, was demonstrated in Kalyuzhny et al. (2015).

However, by introducing a species-specific response to environmental variations, the TNTB finds itself entering the domain of another celebrated mechanism that was suggested to explain species coexistence, the storage effect introduced by Chesson in the 1980s. In particular, Chesson and Warner (1981) considered the "lottery game" in which the fitness of each species, as reflected by the chance of its offspring successfully occupying a vacancy in the community, fluctuates in time. This differential response of species, when superimposed on buffered population growth and covariance between environment relative probability and competition (Chesson, 1994) was shown to stabilize the system. Chesson and Warner showed how 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. Accordingly, the population of rare species increases (their average growth rate is positive just because their relative abundance is low) and the system supports a stable equilibrium: species' abundance fluctuates, but are attracted to a finite value by a restoring force.

Hubbell's NTB, which takes into account demographic noise and speciation but with no environmental noise, provides us with one set of predictions for the patterns characterizing a community, such as species abundance distribution and species richness. The Chesson–Warner lottery game, taking into account only environmental stochasticity (without demographic noise or speciation) suggests another set. What happens under the general model of TNTB, where *all* these elements play a role? What patterns does it predict, and how do they depend on the strength of the storage effect? In Kalyuzhny et al. (2015) the TNTB was presented in the context of a mainland-island model and simulated island dynamics were compared with data from the Barro-Colorado Island (BCI) plot. Here we aim at understanding the metacommunity dynamics of the TNTB and to explore its relationships with both NTB and the lottery game.

To do that, we first revisit the storage effect, using the original Chesson–Warner model. In Section 2 we consider the storage effect for two species, emphasizing the transition it shows from a balanced system, where the abundance of both species fluctuates around one half of the community, and an imbalanced state, with one rare and one frequent species. A deeper analysis of the equilibrium distribution poses a conceptual problem, namely that the result is independent of the amplitude of the environmental variations. This problem is discussed in Section 3, and indicates the necessity of incorporating demographic stochasticity into the model. Before doing that, in Section 4 we consider the original lottery game for communities with many species and discuss its applicability to empirical systems. Finally in Section 5 the TNTB model, in which environmental variations, demographic stochasticity and speciation affect the community, is analyzed. Conclusions are presented in the last section.

2. A lottery game for two species

In this section we study the simplest case, the storage effect in a community with two species playing the lottery game. Since we are ultimately interested in the TNTB, we assume that the fitness of both species is equal when averaged over time (species are equivalent). Note that the scope of the storage effect is wider, and it may stabilize a community even when the average fitnesses are different; we will return to this point in the discussion section.

To provide an intuitive numerical example, let us consider an extremely simple game. Imagine a forest with 100 trees, N_A of species A and $N_B = 100 - N_A$ of species B. For simplicity we assume that there is no spatial structure, seeds and seedlings of both species are all around the forest, with relative frequencies that reflect the relative abundance of adult trees. During every year 20% of the trees are selected at random, independent of their species affiliation, to die (so that the generation time is five years). The gaps that remain after the trees' death are filled by seedlings, where the chance of each seedling to capture the vacancy depends of its relative fitness, with the fitness varying in time. To have equivalent species the temporal fitness is taken to be an independent and identically distributed (i.i.d.) variable, so the chance of a particular species to be the fitter of the two in a certain year is 1/2. Under an extreme, "winner takes all" scenario, the fittest species of a given year captures all the 20 empty slots.

Now let us follow the dynamics. Consider the case where, at the beginning of a certain year, $N_A = 20$ and $N_B = 80$. After the death step, $N_A = 16$ and $N_B = 64$ (this is an average, since trees are picked to die at random, but for our purpose it is sufficient to trace the average). Now there are two options: if the winner of this year is species A, the year ends with $N_A = 36$, $N_B = 64$, while if the fittest species is B, the outcome will be $N_A = 16$, $N_B = 84$. One can easily see that the gain of A when it wins, 16, is higher than the potential gain of B, which increases its population only by four individuals when it wins. By the same token the losses of A when it is the inferior species are smaller then the losses of B in the parallel situation.

While this example is misleading in several respects (in particular the unrealistic winner takes all assumption strongly affects the results), it still provides the basic intuition: although the average fitness of both species is the same, environmental variations provide benefit to the rarer one, as the opportunities for the rare species (when it wins) are greater than those of a common species and its risks (when it loses) are less. Accordingly, an effective stabilizing force acts against any deviation from the 50–50 partition.

Having established this intuition, let us turn to the original two-species model as presented in Chesson and Warner (1981). In this model there is no demographic noise, so the absolute number of individuals has no importance. Accordingly, the variables are