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Stochastic competitive exclusion leads to a cascade of species extinctions

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ABSTRACT

Community ecology has traditionally relied on the competitive exclusion principle, a piece of common wisdom in conceptual frameworks developed to describe species assemblages. Key concepts in community ecology, such as limiting similarity and niche partitioning, are based on competitive exclusion. However, this classical paradigm in ecology relies on implications derived from simple, deterministic models. Here we show how the predictions of a symmetric, deterministic model about the way extinctions proceed can be utterly different from the results derived from the same model when ecological drift (demographic stochasticity) is explicitly considered. Using analytical approximations to the steady-state conditional probabilities for assemblages with two and three species, we demonstrate that stochastic competitive exclusion leads to a cascade of extinctions, whereas the symmetric, deterministic model predicts a multiple collapse of species. To test the robustness of our results, we have studied the effect of environmental stochasticity and relaxed the species symmetry assumption. Our conclusions highlight the crucial role of stochasticity when deriving reliable theoretical predictions for species community assembly.

1. Introduction

Ecological communities are shaped from the complex interplay of four fundamental processes (Vellend, 2010): selection, in the form of species interactions that favor certain species against others; speciation, leading to the appearance of new species, better adapted to the environment; dispersal, which permits spatial propagation of individuals; and ecological drift, a demographic variability in species population numbers due to the stochastic processes that take place. Ecological drift, in particular, has a prevalent role in modern theoretical frameworks in community ecology (Black and McKane, 2012). Accordingly, current approaches reveal the need for process-based, stochastic models that help to understand how ecological communities are assembled and their interaction with environmental factors (Wisz et al., 2013).

Classical community ecology, however, has mainly relied on deterministic community models (see Roughgarden, 1979 and references therein), most of them based on Lotka-Volterra dynamics, although alternatives have been proposed (Schoener, 1974a). There is a long-standing research focus on community assembly models, in which communities are built up through species invasions, and most of them rely on deterministic approaches (Post and Pimm, 1983; Law and Morton, 1993, 1996; Capitán et al., 2009; Capitán and Cuesta, 2011; Capitán, 2011). On the other side, there have been strong theoretical efforts to describe community assemblages in stochastic terms (Hubbell, 2001; Alonso et al., 2008; Rosindell et al., 2011). In certain situations, the results and conclusions derived from deterministic models have been shown to be quite different in the presence of stochasticity (Bolker and Grenfell, 1995; Alonso et al., 2007; Haegeman and Loreau, 2011; Bonachela et al., 2012; Wang et al., 2012).

One of the contexts where the differences between deterministic and stochastic approaches become apparent is related to theoretical formulations of the competitive exclusion principle (Volterra, 1926; Gause, 1934; Hardin, 1960). This principle constitutes a fundamental pillar of community ecology and belongs to the traditional body of ecological theory. It provides a useful theoretical framework to explore how complex species assemblages persist over time. Important concepts such as adaptation to shared niches (Roughgarden, 1979), species limiting similarity (MacArthur and Levins, 1967; Roughgarden, 1974) or niche partitioning (Pielou, 1977; Schoener, 1974b) all are immediate derivations from the principle. Classical approaches predict the maximum degree of species similarity that permit species stable coexistence (MacArthur, 1969, 1970). However, theoretical predictions for limiting similarity often rely on deterministic community models (see MacArthur, 1968; Levin, 1970; Haigh and

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Maynard-Smith, 1972; Chesson, 1990 and Appendix A for a discussion on competitive exclusion based on deterministic approaches), and the relevance of stochasticity, in the form of ecological drift, to species coexistence has remained almost unexplored (with the exception of Turelli (1980)). The relationship between limiting similarity and environmental stochasticity has been studied more thoroughly (May and MacArthur, 1972; Turelli, 1978, 1981).

Recently, we focused on the influence of ecological drift on the similarity of coexisting species via the competitive exclusion principle (Capitán et al., 2015). In that contribution we showed that, in the presence of ecological drift, the maximum degree of similarity that ensures stable coexistence can be significantly lowered when compared to the corresponding limits to similarity derived from deterministic models. If similarity is interpreted in terms of an interspecific competitive overlap (MacArthur and Levins, 1967; Roughgarden, 1974), stochasticity displaces the deterministic threshold towards lower values of the competitive overlap (Capitán et al., 2015). Thus, when stochasticity is considered, the extinction phenomena caused by competitive exclusion takes place at lower values of the competitive overlap (i.e., species have to be more dissimilar to stably coexist in the presence of ecological drift).

Ecological drift becomes a key process determining species coexistence in aspects other than the maximum similarity of co-occurring species. Beyond a more restrictive threshold in competition induced by ecological drift (which was the main result of Capitán et al. (2015)), we here analyze the influence of demographic stochasticity on the extinction mechanism itself, which in principle can lead to either sequential or grouped extinctions as competition strength increases. For that purpose, we considered a deterministic, Lotka-Volterra model and its stochastic counterpart, both of which treat species interactions symmetrically. Whereas the deterministic model predicts the multiple extinction of all the species in the community but one as competition crosses over a certain threshold, in the presence of demographic stochasticity extinctions proceed progressively, in the form of a cascade, as competition increases. The only difference between both approaches is the explicit consideration of ecological drift in the dynamics. In order to derive our conclusions, we developed convenient analytical approximations to the steady-state configurations of the stochastic system for simple species assemblages formed by two or three species. Such approximations help us to partition the set of feasible population numbers into regions associated to coexistence, or the extinction of one, two, or three species. The steady-state probabilities, when aggregated over those regions, unveil the extinction cascade phenomenon. Our main result reveals overlapping windows in competitive strength, at low values related to configurations where the coexistence of three species is the most probable state, intermediate ranges where it is more likely to observe two-species assemblages, and large competition values for which the most probable state is formed by one species or none. We also studied the transition to the deterministic model when demographic stochasticity tends to zero, and our results reveal an abrupt transition to situations compatible with small stochasticity.

To test the robustness of our conclusions, we replaced demographic stochasticity by environmental stochasticity and confirmed that, although the extinction phenomena are qualitatively different, the extinction cascade persists. We also relaxed the assumption of symmetry to assess the effect of stochasticity on deterministic models that not only predict multiple extinctions, as in the fully symmetric scenario, but also lead to both progressive and grouped extinctions for fixed competitive strengths. When stochasticity comes into play, however, the stochastic cascade persists and the expected extinction sequence is qualitatively different from its deterministic counterpart. Thus, the predictions of both models are significantly different in generic, non-symmetric scenarios for species interactions.

The paper is organized as follows: in Section 2 we describe both the deterministic and the stochastic frameworks, the latter based on the formulation of Haegeman and Loreau (2011), and show that the deterministic, symmetric model predicts a multiple species extinction. In Section 3 we start by presenting the analytical approximations for a two-species stochastic community model, and we then extend the procedure to a three-species community. These approximations help us to obtain analytical formulae for the critical points of the steady-state, joint probability distribution of the community. Formulae for saddle points are then used to properly define aggregated probabilities of coexistence, or one-, two-, and three-species extinction, which reveal themselves the sequential decline of species driven by ecological drift. After studying the small stochasticity limit and testing the robustness of our results, we conclude the paper with several implications and prospects (Section 4).

2. Model description

For the sake of simplicity, in this contribution we will focus on the symmetric version of the deterministic Lotka-Volterra competitive dynamics (see Appendix A),

$$\dot{x}_i = rx_i\left(1 - \frac{x_i + \rho\sum_{j\neq i}x_j}{K}\right), \quad i = 1, \ldots, S, \tag{1}$$

where x_i stands for the population density of species i (space is implicitly assumed) and model parameters are uniform and species-independent. Here r stands for an intrinsic, species-independent growth rate, ρ measures interspecific competition, K represents a carrying capacity, and S is the species richness of the community. The dynamics has an interior equilibrium point, $\hat{\mathbf{x}} = (\hat{x}, \ldots, \hat{x})$, where $\hat{x} = K/(1 - \rho + \rho S)$, which is globally stable if and only if $\rho < 1$ (Hofbauer and Sigmund, 1998; Capitán et al., 2015). In the symmetric scenario, the competitive exclusion principle adopts a very simple formulation (see Appendix A for further details on the general, non-symmetric case). A complete stability analysis of the boundary equilibrium points shows that, for $\rho > 1$, all the species become extinct except for just one of them (see Appendix B). As a consequence, competitive exclusion in the symmetric, deterministic model implies the joint extinction of $S - 1$ species.

We now explicitly incorporate ecological drift (demographic stochasticity) in the symmetric scenario in order to show that species are sequentially displaced in the presence of stochasticity due to competitive exclusion, following a cascade of extinctions, as competition strengthens. A standard way to extend deterministic models to incorporate ecological drift is deeply described in Haegeman and Loreau (2011). The state of the system is described by the vector of population numbers n_i at time t, $\mathbf{n}(t) = (n_1(t), \ldots, n_S(t))$. Contrary to the deterministic case, which focuses on population densities $x_i = n_i/\Omega$, Ω being a meaningful measure (area, volume) of the system size, here discrete population numbers are considered. The elementary processes that define the stochastic dynamics (local births and deaths, immigration, and competition) are characterized by probability rates that, in the deterministic limit, yield the Lotka-Volterra Eq. (1). As in Haegeman and Loreau (2011), we choose the following probability rates to model elementary processes:

1. Local births (deaths) of species i occur at a density-independent rate r^+n_i (r^-n_i). We adopt the notation $r = r^+ - r^-$ to represent the net growth rate in the absence of competitors.
2. Immigration of a new individual of species i takes place at a rate μ. Although the deterministic model (1) does not include immigration, dispersal is an important process driving community assembly (Vellend, 2010). In addition, immigration is key for the stochastic process to reach a non-trivial steady-state. We consider here the low-immigration regime, in which the deterministic limit is expected to recover results close to those yielded by Eq. (1), see Capitán et al. (2015).