Coexistence and invasibility in a two-species competition model with habitat-preference

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ABSTRACT

The outcome of competition among species is influenced by the spatial distribution of species and effects such as demographic stochasticity, immigration fluxes, and the existence of preferred habitats. We introduce an individual-based model describing the competition of two species and incorporating all the above ingredients. We find that the presence of habitat preference—generating spatial niches—strongly stabilizes the coexistence of the two species. Eliminating habitat preference—neutral dynamics—the model generates patterns, such as distribution of population sizes, practically identical to those obtained in the presence of habitat preference, provided an higher immigration rate is considered. Notwithstanding the similarity in the population distribution, we show that invasibility properties depend on habitat preference in a non-trivial way. In particular, the neutral model results more invasible or less invasible depending on whether the comparison is made at equal immigration rate or at equal distribution of population size, respectively. We discuss the relevance of these results for the interpretation of invasibility experiments and the species occupancy of preferred habitats.

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1. Introduction

A central problem in community ecology is to understand the ecological forces leading to the observed patterns of coexistence or exclusion of competing species (Ricklefs and Schluter, 1993; Brown et al., 1995). This issue is important for understanding both simple communities made up of few species (Chesson, 2000) and "biodiversity hotspots" with a large number of coexisting species (Leigh et al., 2004). Historically, this problem has been approached at two distinct levels. On the one hand, focus has been put on the detailed mechanisms of interaction between species (e.g., intra- and inter-specific competitions) caused by their differentiation in exploiting resources, resulting in the concept of the ecological niche (Chase and Leibold, 2003). For example, it has been shown how habitat heterogeneity (Beckage and Clark, 2003) or a tradeoff in dispersal range strategies (Bolker and Pacala, 1999) may promote coexistence. An alternative explanation for the observed species richness and distribution is in terms of processes intrinsically due to chance, such as colonization, immigration and extinction (MacArthur and Wilson, 1967), disregarding differences among species.

In recent years, the neutral theory of biodiversity (Hubbell, 1979, 2001; Bell, 2001) considerably developed the latter

approach by explicitly assuming equivalence among species at the individual level. The interest in the neutral theory has been triggered by its ability to successfully predict several biodiversity patterns observed in tropical forests, such as species-abundance distributions in different permanent sampling plots (Bell, 2001; Hubbell, 2001; Volkov et al., 2003) and species-area relations (Durrett and Levin, 1996; Bell, 2001; Hubbell, 2001). Its success underlined the importance of stochasticity (ecological drift) and dispersal limitation in the assemblage of natural communities (Chave, 2004; Alonso et al., 2006), which are now recognized as key ingredient also in niche-based models (Tilman, 2004). However, niche-based models yield predictions for the biodiversity patterns which perform similarly to neutral ones when compared with data (Chave et al., 2002; McGill, 2003; Mouquet and Loreau, 2003; Gilbert and Lechowicz, 2004; Tilman, 2004). This suggests that these patterns tend to average out the dependence on the details of the theory (see also the discussion in Pueyo et al., 2007) and thus cannot be used to discriminate the relative importance of niche-based and neutral forces. In this perspective, the study of dynamical properties such as invasibility can be a promising way to disentangle these effects (Daleo et al., 2009).

To understand the key differences between neutral and non-neutral competition, it is useful to consider models that can be continuously tuned from niche-based to neutral settings by varying some parameters (Chave et al., 2002; Gravel et al., 2006; Adler et al., 2007). An obvious difficulty with this program

comes from the unavoidable complexity of realistic niche-based models (Chase, 2005), where species are not equivalent and the environment is heterogeneous both in space and time. This suggests an approach whereby simplified models with few parameters are studied, for example by making some specific assumptions on how neutrality is violated.

In this paper we study the dynamics of two species A and B that compete for space. The model is devised in such a way that a single parameter controls the overlap between the niches occupied by the two species, from complete—neutral—to no overlap—two independent niches. The model is individual-based and incorporates the basic ingredients of neutral theory: coexistence results from immigration from a metacommunity, balancing demographic stochasticity, which alone would lead to extinction. Niches are introduced in this neutral scenario via preferential habitats: half of the sites in the ecosystem are favorable for the colonization of individuals of one species and the other half are favorable for the other species. The ecological advantage is realized through a biased "lottery" (Chesson and Warner, 1981). We consider a symmetric situation by choosing the same statistical bias, γ, for individuals of species A and B to colonize their respective preferred habitats. When $\gamma = 0$ (no habitat diversification) the model reduces to the voter model (Holley and Liggett, 1975; Cox and Griffeath, 1986), which is a prototype of neutral dynamics. Increasing γ, species acquire an advantage in colonizing some sites and a disadvantage in others. A very large γ eventually leads to segregation of the two species to their preferential habitats. Segregation will be complete when the choice of dispersal allows individuals to reach all their preference sites or incomplete in the presence of dispersal limitation.

The aim of this work is to use this simple model to understand the effect of habitat diversification on coexistence and dynamics of ecological communities. In particular, our concern will be on contrasting the effect of habitat diversification with the neutral model where no preferred habitat exists.

2. Model

We consider an individual based, spatially explicit model of a community made of two competing species A and B with population N_A and N_B, respectively. The community lives in a patch made of $N = L^2$ sites on a square lattice of side L, on which we assume periodic boundary conditions. Each lattice site is occupied by a single individual of one of the two species. For the sake of simplicity, we assume that the patch is saturated, i.e. with no empty sites—each dead individual is immediately replaced, so that the total number of individual is constant, $N_A + N_B = N$. The latter hypothesis is commonly assumed for its convenience (Hubbell, 2001; Chave et al., 2002) and, strictly speaking, corresponds to considering infinite fecundity. However, a finite but reasonably high fecundity would lead to almost-saturated ecosystems with qualitatively similar dynamics (Durrett and Levin, 1996; Chave et al., 2002).

Our main interest here is to study the effect of habitat preference on competition. To this aim, we assign to each site a specificity: half of the sites are favorable (as below specified) to individuals of species A and the other half to individuals of species B. We denote such sites by a and b, respectively. The site specificity can have several different (often concomitant) ecological origins such as abundance of resources, predation pressure (see, e.g., the review by Amarasekare, 2003), and/or environmental conditions such as elevation, temperature, soil moisture or other parameters as in Zillio and Condit (2007) and as suggested by observations (Beckage and Clark, 2003). The net effect of these different mechanisms is here assumed to increase by a factor γ the

chance of individuals to colonize a preferred site. This is illustrated in the top panel of Fig. 1, to be compared with the bottom cartoon which shows the neutral model, without site specificity. Similar models have been proposed also in the context of heterogeneous catalysis (Frachebourg et al., 1995) and social dynamics (Masuda et al., 2010).

For the sake of simplicity, site specificity is randomly assigned at the beginning and left unchanged during the dynamics. Of course, in natural ecosystems, spatial arrangement of sites with a certain specificity will usually be characterized by a certain degree of correlations, which will in general tend to enhance niche effects. In this respect, we expect that our choice will tend to underestimate the effect of habitat preference. Clearly, the model can be generalized by introducing asymmetries, i.e. different γ's for the two species or different fractions of advantageous sites. Here we shall limit our analysis to the simple symmetric case, so that no species has a net advantage and the degree of habitat preference is controlled by a unique parameter.

We also assume a continuous immigration in the patch of individuals A or B at rate v. This inflow is necessary to avoid the drift to extinction of one of the two species.

For any given size L of the patch, which fixes the number of individuals $N = L^2$, the model is controlled by two parameters only: the colonization advantage γ and the immigration rate v. The elementary step of the dynamics is as follows:

 (i) a site is randomly chosen and the individual there residing is killed;
 (ii) with probability $(1 - v)$, the individual is replaced by a copy of one of the four neighbors, chosen via a lottery which gives a competitive advantage (modeled as a weight γ) to individuals having that site as preferred habitat (see the sketch in Fig. 1 and Eqs. (1) and (2) below);
 (iii) with probability v, the individual is replaced by an immigrant. For simplicity, we assume the two species being equipopulated at the metacommunity level, so that the probability of being replaced by an individual of one of the two species is 1/2, apart from the competitive advantage on the specific empty site.
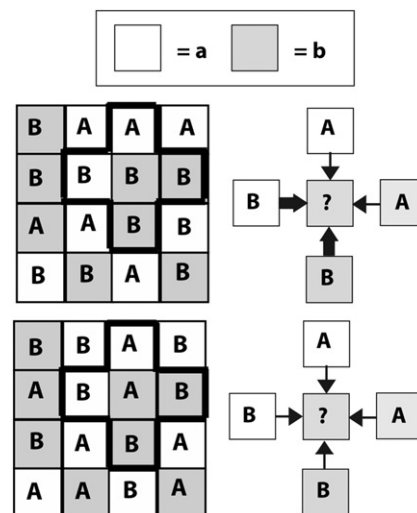

Fig. 1. Sketch illustrating the model with (top) and without (bottom) habitat preference. Two representative configurations of 4×4 systems are shown, white squares are advantageous to A, gray ones to B, and on the right we sketch the lottery dynamics (Eqs. (1) and (2)): the width of arrows represents the habitat preference intensity γ. Notice that in the bottom panel the width of arrows is insensitive to the site specificity.