Alternative stable states and alternative endstates of community assembly through intra- and interspecific positive and negative interactions

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ABSTRACT

Positive and negative interactions within and between species may occur simultaneously, with the net effect depending on population densities. For instance, at low densities plants may ameliorate stress, while competition for resources dominates at higher densities. Here, we propose a simple two-species model in which con- and heterospecifics have a positive effect on per capita growth rate at low densities, while negative interactions dominate at high densities. The model thus includes both Allee effects (intraspecific positive effects) and mutualism (interspecific positive effects), as well as intra- and interspecific competition. Using graphical methods we derive conditions for alternative stable states and species coexistence. We show that mutual non-invasibility (i.e. the inability of each species to invade a population of the other) is more likely when species have a strong positive effect on the own species or a strong negative effect on the other species. Mutual non-invasibility implies alternative stable states, however, there may also be alternative stable states at which species coexist. In the case of species symmetry (i.e. when species are indistinguishable), such alternative coexistence states require that if the positive effect exerted at low densities at the own species is stronger than on the other species, the negative effect at higher densities is also stronger on the own species than on the other species, or, vice versa, if the interspecific positive effects at low densities are stronger than the intraspecific effects, the negative effects at higher densities are also stronger between species than within species. However, the reachability of alternative stable states is restricted by the frequency and density at which species are introduced during community assembly, so that alternative stable states do not always represent alternative endstates of community assembly.

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1. Introduction

How do positive and negative interactions between organisms combine to determine community composition and its dependency on initial population densities? This is an interesting question because evidence suggests that positive and negative interactions occur simultaneously, with the net effect depending on population densities. This is especially true in stressful environments, where organisms may ameliorate harsh conditions while at the same time compete for scarce resources (Bertness and Callaway, 1994; Stachowicz, 2001; Bruno et al., 2003). For instance, in semi-arid grasslands plants increase water availability by reducing evaporation (Maestre et al., 2003), in salt marshes reduced evaporation reduces salinity (Bertness and Yeh, 1994) and in phytoplankton communities under strong light self-shading reduces photoinhibition (Mur et al., 1977; Gerla et al., 2011). Such facilitation occurs both within and between species (Stachowicz, 2001; Fajardo and McIntire, 2011), and may create the possibility of alternative stable states through positive feedback, making community composition dependent on initial densities. If initial densities are important, places with very similar abiotic conditions and the same pool of potential colonizers may develop distinct communities because initial densities differ between places. This may have important consequences for restoration ecology (Suding et al.,

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2004; Young et al., 2005). Also, it may increase diversity between local communities (β-diversity) and increase regional diversity (γ-diversity) even if abiotic heterogeneity is limited and the diversity of each local community (α-diversity) is low (Chase, 2003). Thus, it is well justified to investigate the consequences of positive and negative interactions for the dependency of community composition on initial densities.

Initial densities are determined by the arrival times and densities of species. Thus, arrival times may have a long lasting effect on the species composition of the community, due to priority effects. In such priority effects, early arriving species inhibit the establishment of later arriving species and may cause a type of alternative stable states, where the alternative states are the different communities that eventually develop (Morin, 1999). The archetypal example of a priority effect occurs in the two species Lotka–Volterra competition model (Volterra, 1926; Lotka, 1932) in the case in which interspecific competition exceeds intraspecific competition. In this case, positive feedback of population density on relative fitness causes alternative stable states where in each state only one or the other species survives. Each of the two single species equilibria is stable against invasion by the species that is absent when it is introduced at a low density. This situation is called mutual non-invasibility and in the Lotka–Volterra competition model, mutual non-invasibility is a necessary and sufficient condition for alternative stable states through a priority effect.

To study how species combine to form communities, theoreticians have constructed assembly models (Drake, 1990; Luh and Pimm, 1993; Law and Morton, 1993, 1996; Capitan and Cuesta, 2011). These models simulate community assembly by randomly picking a species from a "regional species pool" and adding it to the community, which is then left to evolve through population growth and interactions within and between populations. This process is repeated until none of the species from the regional pool that are absent in the community can invade. The community is then at an endstate (Law, 1999). For a given species pool, there could in principle be more than one endstate (alternative endstates, Law and Morton, 1993) due to priority effects. Often, assembly models make the simplifying assumptions that species are introduced at a low density and that introductions take place at a low rate relative to the rate at which the resident community develops. As we will show, these assumptions restrict the number of endstates that can be reached through the community assembly process. Therefore, as we will argue, it is important to take the reachability of a community state into account.

In another type of alternative stable states, the eventual outcome is also dependent on initial population densities. The archetypal example here may be the Allee effect (Allee, 1931), in the case where a population has a negative growth rate below a threshold density, and a positive growth rate above this threshold. Positive feedback of population density on the per capita growth rate of the population defines the Allee effect (Stephens et al., 1999). The Allee effect is called strong in the case that the population declines to extinction if it starts off below a threshold density, and weak if there is no such threshold but merely the positive feedback on population growth (Wang and Kot, 2001; Taylor and Hastings, 2005). In the case of a strong Allee effect the alternative stable states correspond to extinction of the population and its survival.

Among the first to model the Allee effect were Volterra (1938) and Kostitzin (1940), who considered decreased fertility at low population densities in sexually reproducing species due to difficulty in finding mates. Both Volterra and Kostitzin found a population density threshold: populations starting off below this threshold go extinct, but above the threshold they survive. This implies a strong Allee effect. Since this pioneering work, many simple models of the Allee effect have been studied in the literature (for an overview, see Boukal and Berec, 2002). Studies of the Allee effect in competing species are relatively rare. The seminal paper of Vandermeer (1973) seems to be the first to study the effects of low density positive intraspecific interactions (i.e. Allee effects), finding a multiplicity of stable states. Similar results were found by Wang et al. (1999) and Ferdy and Molofsky (2002), who found that in two-species communities, Allee effects may destabilize coexistence and lead to alternative stable states. In his purely graphical model, Vandermeer (1973) also considered low density positive interspecific interactions (i.e. mutualisms), again finding multiple stable states as well as oscillatory population dynamics. Since then, authors studying two-species models have emphasized the stabilizing effect of mutualism on coexistence (Zhang, 2003; Zhang et al., 2007). It remains unclear, however, how positive and negative inter- and intraspecific interactions determine community composition when acting simultaneously and how they interact with negative interactions (specifically, competition).

Whether interactions are positive or negative depends on how one defines such interactions (Abrams, 1987) as well as on the context in which they take place. For instance, if one defines interspecific interactions by the effect one population has on the growth rate of another, the sign of the effect may depend on the densities of the species (as pointed out by e.g. Zhang, 2003). On the other hand, one may define the effect one species receives from another species as positive or negative if the one species has a higher or lower density, respectively, when coexisting at equilibrium with the other species than at its single species equilibrium. Using this definition Holland and DeAngelis (2009) showed the effect one species has on the other may change sign as the strength, but not the nature, of their consumer–resource interaction changes. Defining negative and positive effects by differences in population densities can be useful when studying interspecific interactions, however, it does not apply well to intraspecific interactions because it is not clear which equilibrium densities should then be compared.

In the present paper we propose a simple model to explore the effects of positive and negative intra- and interspecific interactions on community composition and its dependency on initial population densities. Here, positive and negative are defined by the effect the interactions have on per capita growth rate, either of individuals of the same species or of another species. The strength of these interactions depends on population densities and turn from positive to negative as densities increase. The model exhibits both strong Allee effects and priority effects. We look for conditions under which these effects lead to alternative stable states, alternative endpoints of community assembly and coexistence. To assess how outcomes change as conditions change we vary the intrinsic growth rate of species from positive to negative values. Furthermore, we discuss how frequency and density of species introductions determine the reachability of alternative stable states and limit the number of community assembly endstates.

2. Model description

To study the effects of positive and negative interactions on community composition, we develop a simple model which is not explicit about the mechanisms that cause the positive and negative interactions. This level of abstractions allows us to arrive at more general conclusions and use graphical methods which illustrate our results. The model is defined as follows. For a community of n species, the population growth rate of the ith species is compactly given by

$$\frac{dN_i}{dt} = N_i \left(r_i + \sum_{j=1}^{n} N_j \left(b_{ij} - \sum_{k=1}^{n} N_k a_{ijk} \right) \right) \quad i = 1, \ldots, n, \quad (1)$$

where t denotes time, N_i denotes the population density of species i, r_i denotes the intrinsic growth rate of species i, which is the