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Research paper

Competitive coexistence and competitive exclusion for a nonlinear community with delay effect and impulsive birth☆

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ABSTRACT

By constructing a population model of multi-species competition, a community with nonlinear interaction relationship is investigated, in which the species' response delay and environmental fluctuation effects (i.e., seasonal fluctuation of resource supplies and species' reproductive activities) on population are considered. Firstly, the conditions about competitive coexistence (i.e., persistence of all species) and competitive exclusion (i.e., only partial of species, but not all, keep persistence) of the community are established, and the underlying ecological mechanism of these results are analyzed. Secondly, by some illustrative examples, the interactive effects of nonlinear competition, species' response delay and environmental fluctuation on the structure of community are explored. It is demonstrated that small response delay and slight deviation of nonlinear competition indexes from 1 have little impact on the coexistence of community, but acute changes have distinct negative influence on community coexistence. This reveals to us that parameter perturbations of natural communities should keep in an appropriate range, which is of great significance in conservation and restoration biology.

1. Introduction

The biodiversity plays significant role in maintaining the service and functioning of ecosystem[1,2]. During the past decades, the ecological consequences caused by biodiversity lose have been the focus of ecological research, the study about the interaction relationship and its intensity between species is an important way to explore the mechanism of biological diversity[3,4].

Predation, competition and reciprocity are the primary interaction patterns among species. Currently, the predator-prey relationships subject have been intensely investigated due to their obvious biological background and practical application values, and the nonlinear scientific method as well as statistical physics theory have been successfully applied to approximate and solve such systems [4–8]. Meanwhile, the competitive interactions between species have also been studied widely. Species competition is divided into the types of hierarchy and non hierarchy via the competition mode of species, the subject of competitive coexistence and the related models of cyclic dominance have been the research topics of the non hierarchical competition problem, its research content involves competitive coexistence, competition association, defensive alliance, and phase transition in cyclical interactions [9–14]. Moreover, competitive coexistence of non hierarchical competition also

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emerge spontaneously in evolutionary settings relevant to the field of social science, as reported in reward and cooperation in the spatial public goods game [15], defense mechanisms of empathetic players in the spatial ultimatum game [16], social network perspective on measurements of dominance hierarchies [17] and cyclic dominance in evolutionary games [18]. Most of them unambiguously support the idea that there must be a minimum amount of intransitivity for the coexistence of all species in the community. This demonstrate that the existence of a certain amount of non-hierarchy competition is a primary condition for the coexistence of competitive species [14,19]. However, there are also many hierarchical competition examples in natural communities, it is of significance to explore the coexistence mechanism of hierarchical competitive relationships. Presently, although the hierarchical competition based on Lotka–Volterra model had been intensively studied, there still some unknown mechanisms to be further explored, such as nonlinear effect of competition, delayed response of species to competition, spatio-temporal heterogeneity of the competition [20–23].

Nonlinear relationship is a ubiquitous phenomenon in the fields of physics, biology, chemistry, information, earth's atmosphere and ocean even social science [17,24]. By the evolutionary game and methods of statistical physics, researches on the phenomena of competitive coexistence in life and social sciences show obvious nonlinearity [10,11,14,19]. However, those results are obtained mainly by the quantitative study of numerical simulation based on the methods of statistical physics, and they lack qualitative theoretical analysis. Meanwhile, although there are some mathematical researches on the nonlinear effect of species competition, they still fail to establish a direct description of the nonlinear mechanism analytically [2,17,24,25]. Therefore, it is of great value to study the nonlinear mechanism of species competition by means of theoretical analysis.

Based on the above reasons, this paper presents a nonlinear community model with hierarchy competitive relationships, and by the qualitative analysis of the mathematical theory, the conditions of nonlinear form of the competitive coexistence and exclusion of community species are established, which can be used to study the problems with the nonlinear relationship in the fields of physics, biology as well as social science.

2. Model

Competition is an important and ubiquitous interaction pattern that describes the quantitative dynamics and evolution of biological organisms [2,4,7]. The primary model to describe the dynamics of species competition is Lotka–Volterra system, which takes the form

$$\dot{x}_i(t) = x_i(t)\left[b_i - d_i - \sum_{j=1}^{n} a_{ij}x_j(t) \right].w \tag{2.1}$$

Where $x_i(t)$ is the density of species i at time t, b_i, d_i are the birth and death rate of species i respectively (i.e., $b_i - d_i$ reflects the intrinsic growth rate of species i), and a_{ij} represents the competitive strength of species j over i. The last term in the bracket expresses the extra death of species i caused by competitive interactions from species j.

The Lotka–Volterra competition model has been widely used to study the assembly and bio-diversity of natural competitive communities [1,3,5,9,21–23], and various coexistence and exclusions criteria have been established [26–30]. However, it simply assumes the linearly competitive mode between species, which is just the first-order Taylor expansions of real species' competitions, meanwhile, it has been confirmed that the nonlinear competitions among species are commonplace in ecological communities, and the growth rate as well as the competition interaction relationship of community species frequently do not conform to the linear way [2,4,14,24]. Thus, if the nonlinear competitions are taken into accounted, one needs to construct the following nonlinear competition model

$$\dot{x}_i(t) = x_i(t)\left[b_i - d_i - \sum_{j=1}^{n} a_{ij}x_j^{\theta_{ij}}(t) \right]. \tag{2.2}$$

Where θ_{ij} describes the nonlinear competition pattern between species. Specifically, θ_{ii} provides a measure of the nonlinearity of intra-specific competitions of species i, and $\theta_{ij}(i \neq j)$ measures the strength of nonlinearly interspecific competitions between species i and j. In comparison with system (3.1), model (2.2) includes two additional competitions, i.e., the accelerating competition ($\theta_{ij} > 1$) and decelerating competition ($\theta_{ij} < 1$) as the density of species j increases, and the Lotka–Volterra system is just a special form of (2.2) with parameters $\theta_{ij} = 1$.

Presently, although various ecological mechanisms about the assembly, stability and bio-diversity of competitive community (2.2) have been established (see [5,9,19,21–23]), the mechanism of competitive coexistence and exclusions of this type community is still not clear, especially when the environmental fluctuations and response time delay of species are taken into accounted. Obviously, the seasonal regularities of physical environments and fertility activity of real-life species make the community parameters to be time-dependent and the growth of community species to be in an impulsive way. While the response time delay is a universal physiological phenomenon in natural species, which makes it is hard for species to respond to the stimuli timely, so the delayed effects of community must be involved when modeling the realistic