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## Gause's principle in interspecific competition of the cyclic predator–prey system



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#### HIGHLIGHTS

- We model the interspecific competition based on the cyclic predator–prey system.
- We consider the average individual ability to prey and the aggregation degree.
- We prove the validity of Gause's Competitive Exclusion Principle.
- We provide a suitable explanation for the biological phenomenon of competition.

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#### ABSTRACT

In this paper, we study the law of survival for species in interspecific competition in the cyclic and predator–prey system. In our model, the successful rate for a predator to prey depends on the individual ability to prey and the two interacting clusters sizes, and the size of a cluster is determined by the aggregation degree between individuals. Experimental results show that only one species can survive when competition occurs on one niche. And which species can survive ultimately depends on the relative relationship between the average individual ability to prey and the aggregation degree between it and its competing species. If competing species have identical values for the average individual ability to prey and the aggregation degree, the species that can survive is determined at random. Therefore, Gause's Competitive Exclusion Principle is correct, but the causes of competing species to survive are different.

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#### 1. Introduction

Two same species cannot coexist indefinitely on the same niche, which refers to the Competitive Exclusion Principle by Gause. The more similar their demands, the greater the intensity of the competition [1]. The validity of this principle has been confirmed by many models [2–8], and evidence can also be found in nature. For example, one population of microorganisms is annihilated from a common habitat in microbial communities [9]. Gause's Competitive Exclusion Principle has always been regarded as a central theme of the ecology, and it attempts to explain the patterns of coexistence for species in the ecosystem. Most of the explanations are based on original niches such as the division of resources and the substitution of roles. Some scientists believe that such a high diversity of species cannot be explained by the certain process itself. Nonetheless, it has been widely accepted that the coexistence of species and the patterns of biodiversity may be a random combination [10].

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The aggregation degree is an important factor for clustering behaviours in the formation of a cluster. Den Boer et al. have studied how the ability of dispersal (the role opposite to the aggregation degree) affects the survival of competing species through observing a region of ground beetles on heathland [11]. Doanh Nguyen-Ngoc et al. have studied the issues of dynamic competition between two competing species and have discussed the relationship between the ability of dispersal and survival [12].

However, the survival success of a species in the process of evolution also depends on the behaviours of other species and they generally exhibit the role of circulation, which can be described as the rock–paper–scissors game [13]. This has been found in nature, for example with invertebrates in coral reefs [14].

Linrong Dong et al. proposed a model for the cyclic role to discuss the behaviours of clustering in a rock–paper–scissors complete mixed system [15].

In this study, we discuss the law of survival for two competing species in one niche based on the two-dimensional rock-paper-scissors system. Experimental results show that Gause's Competitive Exclusion Principle is correct in this system, but the causes of competing species to survive are different.

#### 2. Model

On a  $L \times L$  square lattice, consider an ecosystem including species A, species B, species C and species D. The predator–prey relation is that species A preys on species B and species D, species B and species D prey on species C, and species C preys on species A. Here, species B and species D occupy the same niche. Each cell can accommodate multiple individuals of the same species and only one species can be present in each cell. The predator–prey action happens on two adjacent cells. When individuals of the same species are in two adjacent cells they may gather into a large cluster, and at the same time when an adjacent cell of one species is free its individuals may disperse into this adjacent cell.

The specific rules are as follows:

At time step t, take two adjacent cells, marked as i, j.

- (1) If cells i, j contain species B and species D respectively, there is no action.
- (2) If cells i, j contain the same species Z, they may gather into a large cluster with the probability  $u_Z$  and then concentrate on one cell, while the other cell will be empty. We call  $u_Z$  the aggregation degree of species Z. Here,  $Z \in \{A,B,C,D\}$ .
- (3) If one of cells i, j is free and the other contains species Z individuals, each individual will move to the space with the probability  $\frac{1-u_Z}{2}$ . Here,  $Z \in \{A,B,C,D\}$ .
- (4) If two species in cells i, j have a predator–prey relation, we mark the predator's cluster as X and its size  $S_X(t)$  and prey's cluster as Y and its size  $S_Y(t)$ . Each individual prey's cluster Y may be consumed by the predator's cluster X with the probability  $k_{XY}$ . If n individuals of Y cluster are eaten at time t, we can get  $S_X(t+1) = S_X(t) + n$ ,  $S_Y(t+1) = S_Y(t) n$ . Here,  $k_{XY} = 1 e^{-\frac{v_X S_X}{S_Y}}$  and  $v_X$  represents the average individual ability to prey of species X [15]. Here,  $X \in \{A,B,C,D\}$  and  $Y \in \{A,B,C,D\}$ .

The process above is a Monte Carlo Step. Repeat it for  $\frac{L \times L}{2}$  times as a time step.

#### 3. Results

Take L=100 and the total population size N=10000. Initially, the population size of species A is as same as that of species C and the sum of that of species B and species D. The population sizes of species B and species D are also the same. Each cell contains one individual and these individuals are randomly distributed. Take  $v_A=v_B=v_C=0.5$ ,  $u_A=u_B=u_C=0.5$ . The population size of the four species as a function of time when  $v_D=0.2$ ,  $u_D=0.3$  is shown in Fig. 1.

As shown in Fig. 1, species D is eliminated after a period of time, and the population size of species B reaches the initial total population size of species B and species D, chasing species A and species C in cycle and remaining stable. At this point,  $v_D = 0.2 < v_B = 0.5$ ,  $u_D = 0.3 < u_B = 0.5$ . Compared with species B, the interaction of the lower average individual ability to prey and the lower aggregation degree leads to the eventual extinction of species D.

The population size of the four species as a function of time when  $v_D = 0.7$ ,  $u_D = 0.3$  is shown in Fig. 2.

As shown in Fig. 2, species B is eliminated after a period of time, and the population size of species D closely matches the initial total population size of species B and species D, chasing species A and species C in cycle and remaining stable. At this point,  $v_D = 0.7 > v_B = 0.5$ ,  $u_D = 0.3 < u_B = 0.5$ . Compared with Fig. 1, species D survives when the aggregation degrees of species D are the same, which means the higher average individual ability to prey than that of species B helps species D to exclude species B. In other words, a higher average individual ability to prey exerts a positive effect on the survival of species in competition.

The population size of the four species as a function of time when  $v_D = 0.7$ ,  $u_D = 0.7$  is shown in Fig. 3.

As shown in Fig. 3, species D is eliminated after a period of time, and the population size of species B reaches the initial total population size of species B and species D, chasing species A and species C in cycle and remaining stable. At this point,  $v_D = 0.7 > v_B = 0.5$ ,  $u_D = 0.7 > u_B = 0.5$ . Compared with Fig. 2, species D becomes extinct when the average individual abilities to prey are the same and higher than that of species B, which means a higher aggregation degree is non-beneficial to the survival of species D.

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