

RESEARCH ARTICLE

A Five-Species Jungle Game

Yibin Kang¹, Qiuhui Pan^{1,2}, Xueting Wang¹, Mingfeng He^{1*}

1 School of Mathematical Science, Dalian University of Technology, Dalian, 116024, China, **2** School of Innovation Experiment, Dalian University of Technology, Dalian, 116024, China

* mfhe@dlut.edu.cn

Abstract

In this paper, we investigate the five-species Jungle game in the framework of evolutionary game theory. We address the coexistence and biodiversity of the system using mean-field theory and Monte Carlo simulations. Then, we find that the inhibition from the bottom-level species to the top-level species can be critical factors that affect biodiversity, no matter how it is distributed, whether homogeneously well mixed or structured. We also find that predators' different preferences for food affect species' coexistence.



Introduction

Cyclically dominant systems play a prominent role in nature, especially in explaining biological diversity[1–5]. As the simplest cyclical interaction system that contains three species, the rock-paper-scissors game can explain typical population oscillatory behavior and other indications, i.e., marine benthic systems[6], plant communities[7–11] and microbial populations[2,12–15]. The rock-paper-scissors game is also reflected in the strategy choice on biological methods, for example, the mating strategy of side-blotched lizards[16], the regular oscillations of the numbers of collared lemmings[17] and pacific salmon[18]. In other words, biological diversity can be interpreted by the invasion between species [19, 20]. Extensions of the classical rock-paper-scissors game to more than three strategies have been popular issues in recent research. Avelino *et al.* investigated the three-dimensional predator-prey model with four or five species, showing the spatial distribution of Z_N Lotka-Volterra competition models using stochastic and mean field theory simulations[21]. Dobrinevski *et al.* considered an asymmetric ecological model with four strategies, which contains a three-strategy cycle and a neutral alliance of two strategies, showing that the model exhibits a mobility-dependent selection of either the three-strategy cycle or the neutral pair[22]. Durney *et al.* discussed the evolution of characters of a cyclically competing predator-prey system with four or more species[23]. Feng *et al.* observed self-organization spiral waves of a cyclic five-species system using direct simulations and non-linear partial differential equations[24]. Intoy *et al.* focused on the extinction processes in a cyclic four-species system[25]. In our previous work, we studied the evolution properties of a cyclic five-strategy system with two different invasion routes[26], and the group interactions of the system have been discussed[27–29]. Knebel *et al.* analyzed the coexistence and survival scenarios of Lotka-Volterra networks with both a cyclic four-species system and a cyclic five-species system[30]. Laird *et al.* provided numbers for possible competitive topologies for a cyclic

OPEN ACCESS

Citation: Kang Y, Pan Q, Wang X, He M (2016) A Five-Species Jungle Game. PLoS ONE 11(6): e0157938. doi:10.1371/journal.pone.0157938

Editor: Gui-Quan Sun, Shanxi University, CHINA

Received: February 28, 2016

Accepted: June 7, 2016

Published: June 22, 2016

Copyright: © 2016 Kang et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the paper.

Funding: The authors have no support or funding to report.

Competing Interests: The authors have declared that no competing interests exist.

five-species system, showing the different coexistences[31]. Li *et al.* analyzed the evolution properties of the N-species Jungle game, which is a special cyclic competing system by mean-field theory[32]. Spatial effects and time delay have influences on cyclically dominant systems, Sun *et al.* have made important contributions in these fields[33–40].

Cyclic dominance of species plays an important role in biology system in nature[2,16]. The higher-level species invade the lower-level species; however, the bottom-level species may invade the top-level species. For example, the lowest level can be thought of as bare space, which is invaded by grasses and other pioneering species, which are invaded in turn by small shrubs and finally forest trees. The forest is destroyed by fire to return to the bare space condition.

Cyclic dominance of strategies also plays an important role in sociology, e.g. four strategies ALLC, ALLD, TFT(Tit For Tat) and WSLS(Win Stay Lose Shift) in a repeated prisoner's dilemma[41]. Strategy ALLD can invade strategies WSLS and ALLC, and be invaded by strategy TFT, just like the top-level species in our model. Strategy WSLS can invade strategies ALLC and TFT, and be invaded by strategy ALLD, just like the second-level species in our model. Strategy ALLC can invade strategy TFT, and be invaded by strategies ALLD and WSLS, just like the third-level species in our model. Strategy TFT can invade strategy ALLD, and be invaded by strategies WSLS and ALLD, just like the bottom-level species in our model. From this we know that strategies ALLD and WSLS can both invade two different strategies. However, as strategy WSLS can be invaded by strategy ALLD, strategy ALLD has the higher level than strategy WSLS. Similarly, strategy ALLC has the higher level than strategy TFT.

In our paper, we investigate the five-species Jungle game in the framework of evolutionary game theory. The Jungle game are based on a traditional Chinese board game. We investigate the coexistence of the species using mean-field theory and Monte Carlo simulation and discuss the biological significance of two special examples. In Ref. [32], the authors find that species may become extinct in seconds without considering the impact of the changing invasion rate on the system, which is not valid for ecological systems in nature. In our paper, we find that the coexistence of species is related to the invasion rate between species. Species are well mixed in mean-field theory; we give all of the appropriate functional relationships of invasion rates for every coexistence state of the system, respectively. In the Monte Carlo simulation, we discuss the impacts of different invasion rates on the system. We define the primary food of a chosen species as the next-level species. Other species, not the chosen species and its next-level species, are the sub-food of the chosen species. We find that predators' different preferences for food affect the coexistence of species. The more the predation rate on predators' sub-prey approaches 1.149 times the rate on the primary prey, the lower is the area in the parameter space (p_2, s) that makes all five species coexist.

Model

The traditional Chinese board game, the Jungle game, ranks animals on the board as 1, 2, The animal ranking in our paper, from strongest to weakest, is S_1 -Elephant, S_2 -Tiger, S_3 -Wolf, S_4 -Cat and S_5 -Rat. The above jungle game between individuals of five species S_1, S_2, S_3, S_4 and S_5 is established to describe cyclic competition and reproduction according to the following

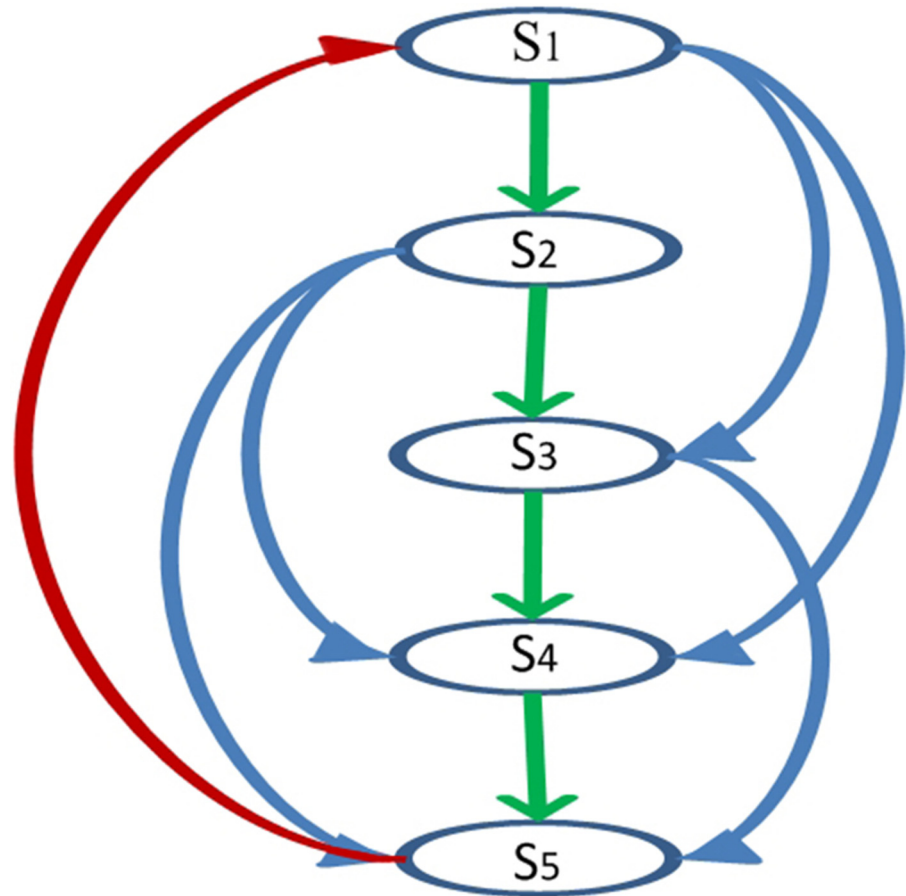
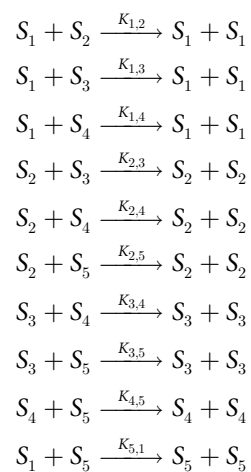


Fig 1. (color online). The relationships of five species in the Jungle game. Arrows point from predator to prey. S_1 and S_2 can prey three species and be hunted by one species; S_3 can prey two species and be hunted by two species; S_4 and S_5 can prey one species and be hunted by three species.

doi:10.1371/journal.pone.0157938.g001

invasion rules (see Fig 1):



Species S_1 invades S_2 , S_3 and S_4 with invasion rates $K_{1,2}$, $K_{1,3}$ and $K_{1,4}$; Species S_2 invades S_3 , S_4 and S_5 with invasion rates $K_{2,3}$, $K_{2,4}$ and $K_{2,5}$; Species S_3 invades S_4 and S_5 with invasion rates

$K_{3,4}$ and $K_{3,5}$; Species S_4 invades S_5 with invasion rate $K_{4,5}$; Species S_5 invades S_1 with invasion rate $K_{5,1}$. In the traditional Chinese board game rules, the rat can capture the elephant, as it can crawl in the elephant's ear and gnaw at its brain. Here, $K_{i,j}$ means the rate that species S_i invades species S_j .

Mean-Field Theory

Considering what happens without the spatial constraints in effect, we study a well-mixed system using mean-field approximation. The dynamics of the system are described by the following equations, with the densities x_i of species S_i :

$$\begin{aligned}
 \partial_t x_1 &= x_1(K_{1,2}x_2 + K_{1,3}x_3 + K_{1,4}x_4 - K_{5,1}x_5) \\
 \partial_t x_2 &= x_2(-K_{1,2}x_1 + K_{2,3}x_3 + K_{2,4}x_4 + K_{2,5}x_5) \\
 \partial_t x_3 &= x_3(-K_{1,3}x_1 - K_{2,3}x_2 + K_{3,4}x_4 + K_{3,5}x_5) \\
 \partial_t x_4 &= x_4(-K_{1,4}x_1 - K_{2,4}x_2 - K_{3,4}x_3 + K_{4,5}x_5) \\
 \partial_t x_5 &= x_5(K_{5,1}x_1 - K_{2,5}x_2 - K_{3,5}x_3 - K_{4,5}x_4)
 \end{aligned} \tag{1}$$

Let $A = K_{1,3}K_{2,5} + K_{2,3}K_{5,1} - K_{1,2}K_{3,5}$, $B = K_{1,4}K_{2,5} + K_{2,4}K_{5,1} - K_{1,2}K_{4,5}$ and $C = K_{1,4}K_{3,5} + K_{3,4}K_{5,1} - K_{1,3}K_{4,5}$, if $ABC \neq 0$, we obtain the following conclusions (for proof, see [Appendix](#)):

1. When $A > 0$ and $B > 0$, three species, S_1 , S_2 and S_5 , can stably coexist and the dynamic system is equivalent to a stable rock-paper-scissors system with three species.
2. When $A < 0$ and $C > 0$, three species, S_1 , S_3 and S_5 , can stably coexist and the dynamic system is equivalent to a stable rock-paper-scissors system with three species.
3. When $B < 0$ and $C < 0$, three species, S_1 , S_4 and S_5 , can stably coexist and the dynamic system is equivalent to a stable rock-paper-scissors system with three species.
4. When $AB < 0$ and $AC > 0$, all five species can stably coexist in this system.

In summary, three rock-paper-scissors topological structures, $S_1S_2S_5$, $S_1S_3S_5$ and $S_1S_4S_5$, may emerge with different values of invasion rates. Moreover, all five species can stably coexist when the invasion rates meet the conditions $AB < 0$ and $AC > 0$.

Example 1

In this five-species jungle game, 10 parameters are used to describe the invasion rates between species. Already in this low dimension it is difficult to draw intuitive conclusions. Thus, we simplify the model to explore the biological significance and it should be noted that we do not consider the trophic loss in this model. In such a jungle game, species S_1 is located on the top level of the food chain, and species S_5 is located on the bottom of the food chain. Each species feeds on the species at lower levels. We define the primary food of a chosen species as the next-level species. Other species, not the chosen species and its next-level species, are the sub-food of the chosen species. The bottom-level species have an inhibitory effect on the top-level species; thus, the bottom-level species invade the top-level species. For example, the lowest level can be thought of as bare space, which is invaded by grasses and other pioneering species, which are invaded in turn by small shrubs and finally forest trees. The forest is destroyed by fire to return to the bare space condition.

Let $K_{i,i+1} = 1$ ($i = 1, 2, 3, 4$) denote the predation rate of a species feeding on its primary food. $K_{5,1} = s$ denotes the inhibitory rate from the bottom-level species to top-level species and

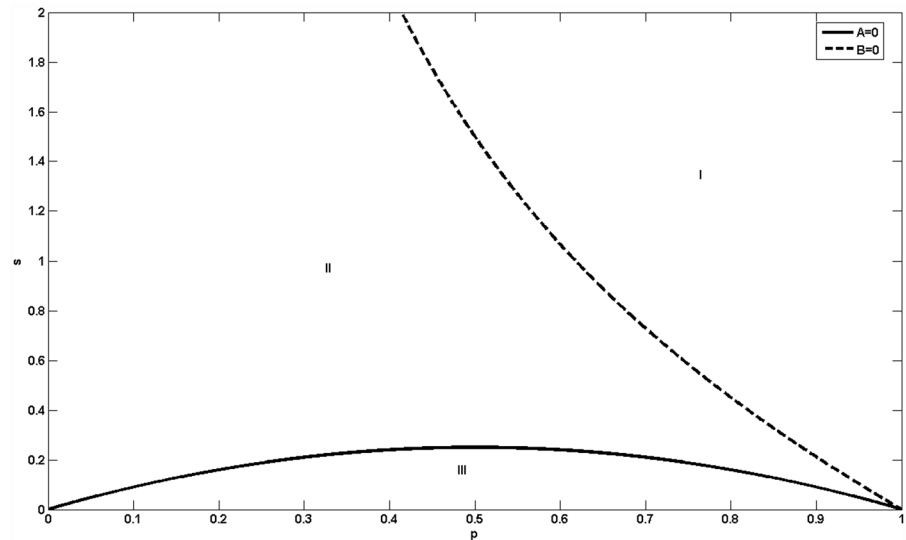


Fig 2. The biodiversity of the Jungle game in the first example. Species S_1, S_2 and S_5 coexist in region I; all five species coexist in region II; and species S_1, S_4 and S_5 coexist in region III.

doi:10.1371/journal.pone.0157938.g002

$p, p < 1$ denotes the predation rate of a species feeding on its secondary food, and we have $A = C = p^2 - p + s$ and $B = p^2 + sp - 1$. Fig 2 shows the biological diversity of the jungle game.

In Fig 2, the solid line denotes $A = C = 0$ and the dashed line denotes $B = 0$. In region I, species S_1, S_2 and S_5 coexist in the system with $A > 0$ and $B > 0$. In region II, all five species coexist with $AB < 0$ and $AC > 0$. In region III, species S_1, S_4 and S_5 coexist with $B < 0$ and $C < 0$. We can go further to say that if we do not distinguish between the species' primary food and sub-food (when $p = 1$), the system will degenerate into three species (the two top-level species and the bottom-level species) regardless of the value s , as explained in [32]. If species can only feed on their primary food, all five species coexist as the conclusion of the rock-paper-scissors game with more than three strategies. In our work, we investigate the difference between the predation rates of species capturing their primary and secondary food. Because $0 < p < 1$, the coexistence of species relates to the inhibitory strength from the bottom-level species to the top-level species. If $s > 1/p - p$, the two top-level species S_1, S_2 and the bottom-level species S_5 coexist. If $s < -p^2 + p$, the top-level species S_1 and the two bottom-level species S_4, S_5 coexist. When $1/p - p < s < -p^2 + p$, all five species coexist.

Example 2

Similar with Example 1, we do not consider the trophic loss in this model. Let $K_{i,i+1} = 1$ ($i = 1, 2, 3, 4$), $K_{i,i+2} = p_1$ ($i = 1, 2, 3$), $K_{i,i+3} = p_2$ ($i = 1, 2$), $K_{5,1} = s$; we then obtain $A = C = 0 \Leftrightarrow s = p_1(1 - p_2)$ and $B = 0 \Leftrightarrow s = p_1^{-1}(1 - p_2^2)$.

In the parameter space (p_2, s) , the curve $A = 0$ is a straight line through points $(0, p_1)$ and $(1, 0)$. The curve $B = 0$, through points $(0, p_1^{-1})$ and $(1, 0)$, is a parabola with its axis of symmetry lying on the y-axis.

Fig 3(a) shows the coexistence of the system when $p_1 \leq 1$. As we can see from the figure, when $p_2 \geq 1$, species S_1, S_2 and S_5 coexist in the system regardless of the value of parameter s . When $p_2 < 1$, the coexistence of the system is related to the value of s . A larger or smaller s may lead to the extinction of two species. If the value of s is appropriate, all five species can coexist, as shown in Fig 3(a).

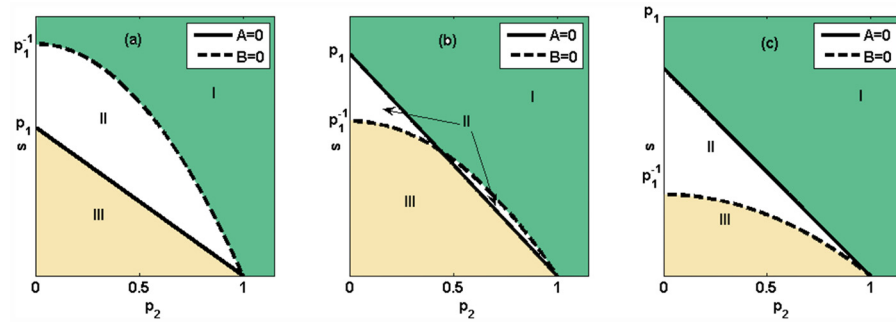


Fig 3. The biodiversity of the Jungle game in the second example. (a) $p_1 \leq 1$; (b) $1 < p_1 < \sqrt{2}$; (c) $p_1 \geq \sqrt{2}$. Species S_1, S_2 and S_5 coexist in region I (green); all five species coexist in region II (white); and species S_1, S_4 and S_5 coexist in region III (yellow).

doi:10.1371/journal.pone.0157938.g003

Fig 3(b) shows the coexistence of the system when $1 < p_1 < \sqrt{2}$. As we can see from the figure when $p_2 \geq 1$, species S_1, S_2 and S_5 coexist in the system no matter what the value of parameter s . When $p_2 < 1$ and $p_2 \neq p_1^2 - 1$, the coexistence of the system is related to the value of s . A larger or smaller s may lead to the extinction of two species. When $p_2 \neq p_1^2 - 1$, if $s > p_1(2 - p_1^2)$, species S_1, S_4 and S_5 coexist in the system.

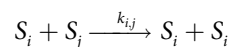
When $p_1 \geq \sqrt{2}$, we can see the coexistence of the system from Fig 3(c). As shown in the figure, species S_1, S_2 and S_5 coexist in the system regardless of the value of parameter s . When $p_2 < 1$, the coexistence of the system is related to the value of s . A larger or smaller s may lead to the extinction of two species. If the value of s is appropriate, all five species can coexist, as shown in Fig 3(c).

Let *Area* denote the area of the coexistence region of five species. When $p_1 \leq 1$, we get $\frac{\partial Area}{\partial p_1} < 0$. When $p_1 \geq \sqrt{2}$, we get $\frac{\partial Area}{\partial p_1} > 0$. When $1 < p_1 < \sqrt{2}$, the relationship between *Area* and p_1 is shown in Fig 4. In other words, there exists $P \approx 1.149$ making the smallest *Area* at $p_1 = P$. When $1 < p_1 < \sqrt{2}$, we get

$$Area = \int_0^1 |p_1(1 - p_2) - p_1^{-1}(1 - p_2^2)| dp_2 = -\frac{1}{3}p_1^5 + 2p_1^3 - \frac{7}{2}p_1 + 2p_1^{-1}$$
. As $\frac{\partial Area}{\partial p_1} \Big|_{p_1=P} = 0$, we know that P^2 is a root of the equation $10x^3 - 36x^2 + 21x + 10 = 0$. Thus, we can go further and say that the closer the predation rate on predators' sub-prey is to 1.149 times the rate on the primary prey, the lower is the area in the parameter space (p_2, s) that makes all five species coexist.

Simulation

Ecological systems exhibit spatial structure; thus, we discuss the Jungle game within the spatial structure. We consider a spatial environment as one that puts individuals on a square lattice of linear size L with periodic spatial boundary conditions. Each site can only be occupied by one individual. Interactions between individuals are based on Monte Carlo simulation. Once we randomly place individuals from five species on the lattice, we stochastically choose one individual and one of its Moore neighbors. If the chosen two species are different, letting predator (S_i) replace prey (S_j) at the probability $k_{i,j}$ we obtain



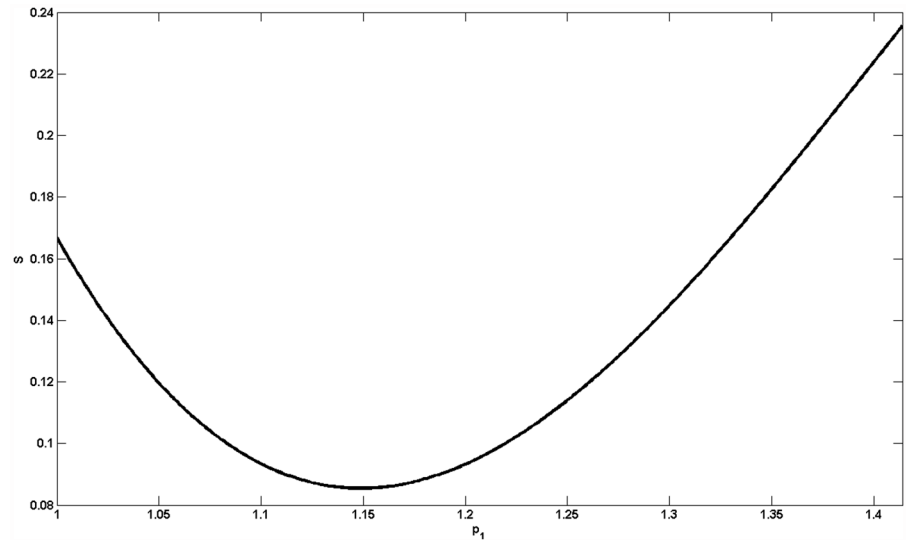


Fig 4. The area of region II in Fig 3 with different p_1 . There exists $P \approx 1.149$ making the smallest area at $p_1 = P$. When $p_1 < P$, the area decreases with the increasing p_1 ; when $p_1 > P$, the area increases with the increasing p_1 .

doi:10.1371/journal.pone.0157938.g004

where $k_{i,j} = \frac{K_{i,j}}{\sum_{s,t} K_{s,t}}$. The above steps are repeated $L \times L$ times to complete one Monte Carlo step.

Setting $L = 200$ and $k_{i,j} = 1$, we obtain the steady-state densities of different species evolving through time, as shown in Fig 5. We can see from Fig 5 that species S_3 and S_4 became extinct quickly and that the remaining densities of species S_1 , S_2 and S_5 are periodic fluctuations forming a rock-paper-scissors game when setting all values of the invasion rate equal. This result is the same as the results from both Mean-field theory and Ref. [32].

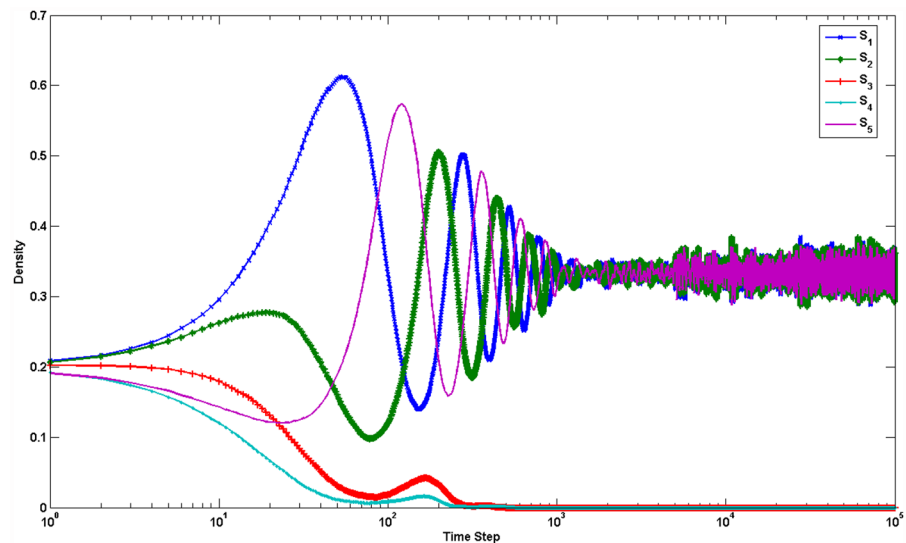


Fig 5. (color online) Densities of five species in Monte Carlo simulation. $L = 200, k_{i,j} = 1$. After about 500 time steps, the species S_4 and S_3 extinct and species S_1 , S_2 and S_5 coexist.

doi:10.1371/journal.pone.0157938.g005

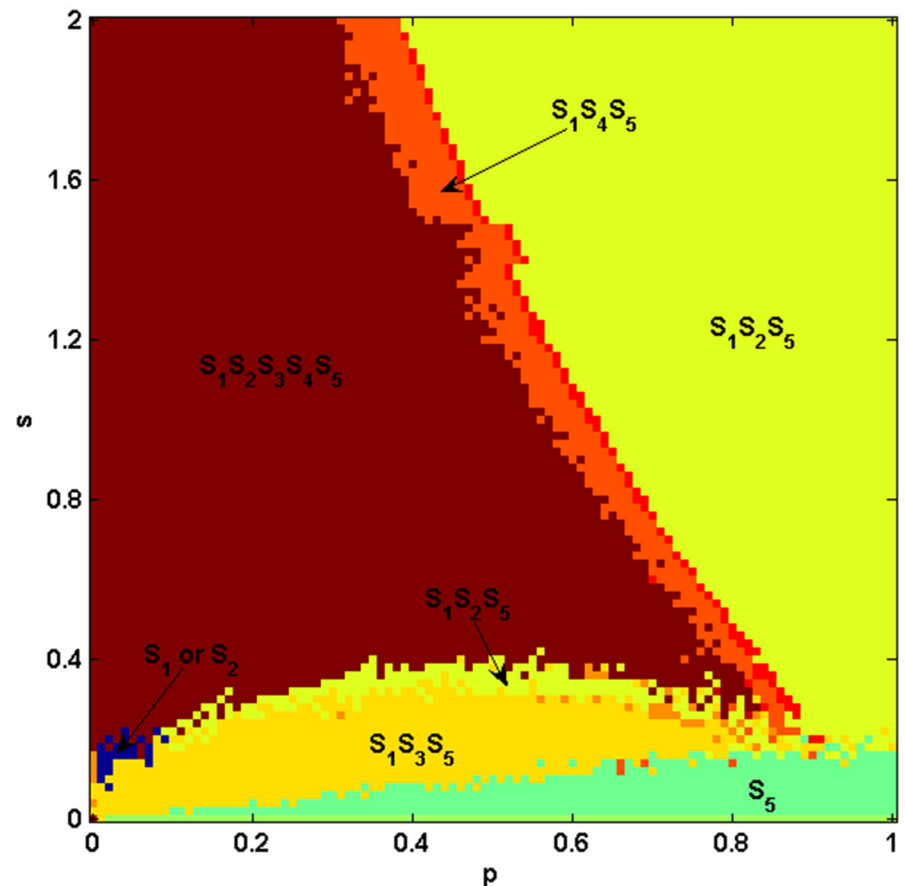


Fig 6. (color online) Coexistence of species in example 1 using Monte Carlo simulation. $L = 400$. All five species coexist in the red region. Species $S_1S_4S_5$ coexist in the orange region. Species $S_1S_2S_5$ coexist in the light yellow region. Species $S_1S_3S_5$ coexist in the deep yellow region. Only S_1 or S_2 remains in the blue region. Only S_5 remains in the green region.

doi:10.1371/journal.pone.0157938.g006

We traverse the parameters s and p in example 1. Fig 6 shows the coexistence of species in the Jungle game after 10^5 Monte Carlo steps under one run. By comparing Figs 3 and 6, we know the coexistence of species in the Monte Carlo simulation, which, considering spatial structure, is different from cases in Mean-field theory, in which species are well mixed. In Mean-field theory, there are only four states of the coexistence of species: all five species coexist, species $S_1S_2S_5$ coexist, species $S_1S_3S_5$ coexist and species $S_1S_4S_5$ coexist. However, in the Monte Carlo simulation with the spatial structure, when the parameter s is small, species S_5 may occupy the whole system. Species S_1 or S_2 also may occupy the whole system when both s and p are small. We also know that the restriction from the bottom-level species to the top-level species has significant influences on the coexistence of species in the ecosystem, both in Mean-field theory and in Monte Carlo simulations. Then, we study the influence of population size on the fluctuation of species' densities. As shown in Fig 7, the fluctuations of species' densities and the coexistence of species are influenced by different population sizes of species. Species S_3 and S_4 go extinct after 10,000 MCS since $L = 100$, see Fig 7a. When $L \geq 200$, five species can coexist, as shown in Fig 7b, 7c, and 7d. At this time, the fluctuations of species' densities decrease with the increasing L . Huge population size reduces the fluctuation of density. Similar with Ref. [29], the population size has impact on the coexistence of the system. Fig 8 shows the

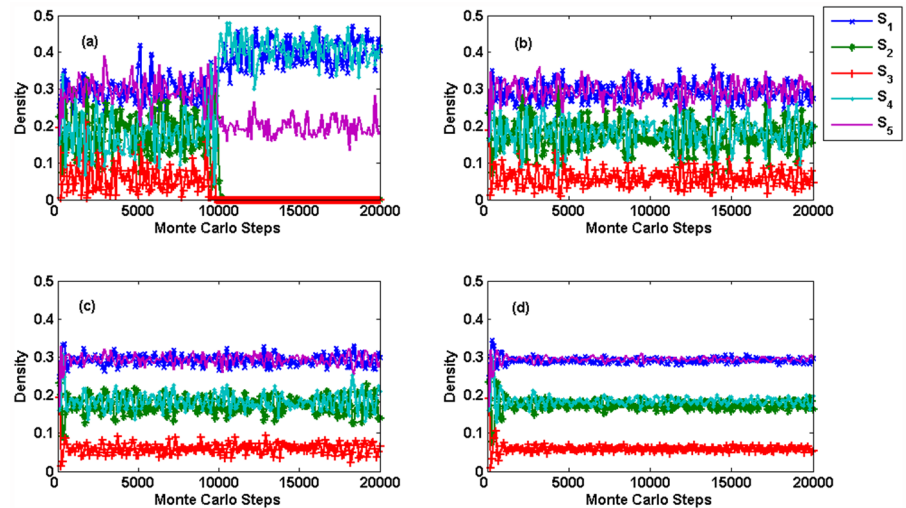


Fig 7. (color online) $p = 0.5$, $s = 1.2$. Densities of species under different population sizes. (a) $L = 100$. (b) $L = 200$. (c) $L = 400$. (d) $L = 800$. (a) Species S_2 and S_3 extinct after 10000 MCS, species S_1 , S_4 and S_5 coexist. In (b), (c) and (d), all the five species coexist, the densities fluctuation decreases with the increasing L .

doi:10.1371/journal.pone.0157938.g007

spatial patterns of species under different population sizes L . We can see from Figs 7 and 8 that the size of habitat directly influences the biodiversity of the Jungle game. We can go further to say that the loss of habitat may be the major factor leading to the extinction of species.

Conclusions

We construct a cyclic, five-species competing model with the special topology as the Jungle game. In this model, species are located on different levels. The top-level species can invade all

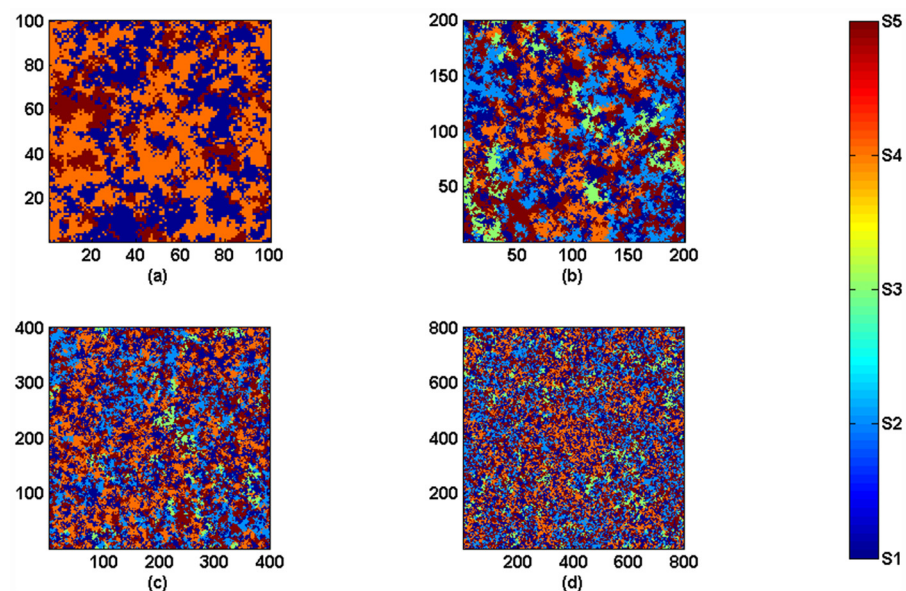


Fig 8. (color online) $p = 0.5$, $s = 1.2$. Spatial patterns after 20000 MCS under different population sizes. (a) $L = 100$. (b) $L = 200$. (c) $L = 400$. (d) $L = 800$. Deep blue represents species S_1 , light blue represents species S_2 , green represents species S_3 , orange represents species S_4 and red represents species S_5 .

doi:10.1371/journal.pone.0157938.g008

other species except the bottom-level species. The bottom-level species can only invade the top-level species. Other species can invade the levels lower than themselves. We discuss the system stabilities using mean-field theory. The results imply that invasion rates can affect species' coexistence. We also find that the coexistence of species is related to the invasion rate between species. All five species can coexist under specific invasion rates. This result is different from the results in Ref. [32], which did not consider the impact of a changing invasion rate on the system.

In the first simplified model, our findings have biological significance. In the five-species jungle game, if all of the species only feed on their primary food source, all five species can coexist. If the species have the same invasion rates for their primary and secondary food sources, two species become extinct, and the two top-level species and the bottom species remain and constitute a stable rock-paper-scissors game. If the species prefer to invade the primary food rather than the secondary food, the coexistence of the system relies on the invasion rate by which the bottom-level species inhibits the top-level species. In nature, there can be different ways that the bottom-level species can invade the top-level species. For instance, the forest is destroyed by fire to return to the bare space condition. We find that inhibition from the bottom-level species to the top-level species can be a critical factor that affects biodiversity.

In the second simplified model, we divided the species' food into three levels. The neighbor-level food is the primary food of a species. Then, the next-level food is the secondary food, followed by the third food. We find that if the predator prefers its third food rather than its primary food, the system of five species cannot coexist. When a predator prefers to hunt its primary prey than its third-level prey, the biodiversity in the Jungle game depends on the invasion rate that the bottom-level species invade the top-level species. Excessive high or low invasion rate will lead to the extinction of species. If a predator prefers to hunt its primary prey than its second-level prey or the preference for a predator to hunt its second-level prey is $\sqrt{2}$ times than that to hunt its primary prey, the decreasing preference for a predator to hunt its third-level prey makes the increasing invasion rate range which made the all species in the system stable coexistence. If a predator prefers to hunt its second-level prey than its primary prey or the preference for a predator to hunt its second-level prey is $\sqrt{2}$ times lower than that to hunt its primary prey, the invasion rate range which made the all species in the system stable coexistence is tiny. The more the predation rate on predators' sub-prey approaches 1.149 times the rate on the primary prey, the lower is the possibility that all five species coexist.

We find more coexistence cases of species in the Monte Carlo simulation, considering the spatial structure: all five species coexist, species $S_1S_2S_5$ coexist, species $S_1S_3S_5$ coexist, species $S_1S_4S_5$ coexist, only S_1 exists, only S_2 exists, or only S_5 exists. The coexistence of species is related to the fluctuation of density and the population size. However, the restriction probability s from bottom-level species to top-level species has significant influences on the coexistence of species in the ecosystem, both when considering spatial structure and when not considering spatial structure.

Although we do not attempt to explain the multiple-species ecosystem in the association of species, the cyclically dominant associations are worth further research [29, 42–44]. There are three three-species associations, $S_1S_2S_5$, $S_1S_3S_5$, and $S_1S_4S_5$, and one five-species association, $S_1S_2S_3S_4S_5$, in our model. Additionally, three species may occupy the entire system by themselves: S_1 , S_2 and S_5 . Thus, the cyclically dominant association is also an important way to study the Jungle game. Similarly, it should be noted that the models we mentioned in our paper are based on zero-sum games, thus they cannot immediately apply to food-chain models which include trophic loss. Therefore, the Jungle game with the trophic loss is worth to research. In other population dynamics systems, the invasions between species and the transformation relationships are similar to the Jungle game. For example, in some epidemiological models [34, 36], the susceptible ones are similar to the bottom-level species in our paper, the immune ones are

similar to the top-level species in our paper. The methods and results we got may be helpful to the researches on these fields.

Appendix

1. Assume $A > 0$ and $B > 0$. Setting

$$V(x_1, x_2, x_3, x_4, x_5) = x_1^{K_{2,5}} x_2^{K_{1,5}} x_5^{K_{1,2}},$$

Thus,

$$\frac{dV}{dt} = V \left(K_{2,5} \frac{1}{x_1} \frac{dx_1}{dt} + K_{1,5} \frac{1}{x_2} \frac{dx_2}{dt} + K_{1,2} \frac{1}{x_5} \frac{dx_5}{dt} \right) = V(Ax_3 + Bx_4) \geq 0.$$

As $V \leq 1$ and $|\frac{d^2V}{dt^2}| < \infty$, we know that the subspace $\{\frac{dV}{dt} = 0\}$ which means $\{x_3 = x_4 = 0\}$ is the invariant subspace of (Eq 1). Based on LaSalle's invariance principle, the subspace $\{x_3 = x_4 = 0\}$ is also the global attractor of (Eq 1). Hence, species S_3 and S_4 die out.

As $V(t)$ monotonic is non-decreasing, species S_1 , S_2 and S_5 will not become extinct if they exist at the beginning.

2. Assume $A < 0$ and $C > 0$. Setting

$$V_2(x_1, x_2, x_3, x_4, x_5) = x_1^{K_{3,5}} x_3^{K_{5,1}} x_5^{K_{1,3}},$$

Thus,

$$\frac{dV_2}{dt} = V_2 \left(K_{3,5} \frac{1}{x_1} \frac{dx_1}{dt} + K_{5,1} \frac{1}{x_3} \frac{dx_3}{dt} + K_{1,3} \frac{1}{x_5} \frac{dx_5}{dt} \right) = V_2(-Ax_2 + Cx_4) \geq 0.$$

As $V_2 \leq 1$ and $|\frac{d^2V_2}{dt^2}| < \infty$, we know that the subspace $\{\frac{dV_2}{dt} = 0\}$ which means $\{x_2 = x_4 = 0\}$ is the invariant subspace of (Eq 1). Based on LaSalle's invariance principle, the subspace $\{x_2 = x_4 = 0\}$ is also the global attractor of (Eq 1). Hence, species S_2 and S_4 die out.

As $V_2(t)$ monotonic is non-decreasing, species S_1 , S_3 and S_5 will not become extinct if they exist at the beginning.

3. Assume $B < 0$ and $C < 0$. Setting

$$V_3(x_1, x_2, x_3, x_4, x_5) = x_1^{K_{4,5}} x_4^{K_{5,1}} x_5^{K_{1,4}},$$

Thus,

$$\frac{dV_3}{dt} = V_3 \left(K_{4,5} \frac{1}{x_1} \frac{dx_1}{dt} + K_{5,1} \frac{1}{x_4} \frac{dx_4}{dt} + K_{1,4} \frac{1}{x_5} \frac{dx_5}{dt} \right) = V_3(-Bx_2 - Cx_3) \geq 0.$$

As $V_3 \leq 1$ and $|\frac{d^2V_3}{dt^2}| < \infty$, we know that the subspace $\{\frac{dV_3}{dt} = 0\}$ which means $\{x_2 = x_3 = 0\}$ is the invariant subspace of (Eq 1). Based on LaSalle's invariance principle, the subspace $\{x_2 = x_3 = 0\}$ is also the global attractor of (Eq 1). Hence, species S_2 and S_3 die out.

As $V_3(t)$ monotonic is non-decreasing, species S_1 , S_4 and S_5 will not become extinct if they exist at the beginning.

4. Assume $AB < 0$ and $AC > 0$.

Let $D = K_{1,4}K_{2,3} + K_{1,2}K_{3,4} - K_{1,3}K_{2,4}$, $E = K_{2,3}K_{4,5} + K_{2,5}K_{3,4} - K_{2,4}K_{3,5}$.

If $A > 0$, we set

$$V_4(x_1, x_2, x_3, x_4, x_5) = x_1^E x_2^C x_3^{-B} x_4^A x_5^D,$$

Thus,

$$\frac{dV_4}{dt} = V_4 \left(E \frac{1}{x_1} \frac{dx_1}{dt} + C \frac{1}{x_2} \frac{dx_2}{dt} - B \frac{1}{x_3} \frac{dx_3}{dt} + A \frac{1}{x_4} \frac{dx_4}{dt} + D \frac{1}{x_5} \frac{dx_5}{dt} \right) = 0.$$

As $-B > 0, C > 0$,

$$D = \frac{K_{1,4}K_{2,4}A + K_{1,2}K_{2,4}C - (K_{1,2}K_{3,4} + K_{1,4}K_{2,3})B}{K_{2,4}K_{5,1} - B} > 0$$

and

$$E = \frac{K_{2,4}K_{4,5}A + K_{2,4}K_{2,5}C - (K_{2,5}K_{3,4} + K_{2,3}K_{4,5})B}{K_{2,4}K_{5,1} - B} > 0,$$

we can know that species S_1, S_2, S_3, S_4 and S_5 will not become extinct if they exist at the beginning.

If $A < 0$, we set

$$V_5(x_1, x_2, x_3, x_4, x_5) = x_1^{-E} x_2^{-C} x_3^B x_4^{-A} x_5^{-D},$$

Thus,

$$\frac{dV_5}{dt} = V_5 \left(-E \frac{1}{x_1} \frac{dx_1}{dt} - C \frac{1}{x_2} \frac{dx_2}{dt} + B \frac{1}{x_3} \frac{dx_3}{dt} - A \frac{1}{x_4} \frac{dx_4}{dt} - D \frac{1}{x_5} \frac{dx_5}{dt} \right) = 0.$$

As $B > 0, -C > 0$,

$$-D = -\frac{K_{3,5}(K_{1,4}K_{2,4}A + K_{1,2}K_{2,4}C - (K_{1,2}K_{3,4} + K_{1,4}K_{2,3})B)}{K_{2,3}K_{4,5}K_{5,1} + K_{2,5}K_{3,4}K_{5,1} - K_{4,5}A - K_{2,5}C} > 0$$

and

$$-E = -\frac{K_{3,5}(K_{2,4}K_{4,5}A + K_{2,4}K_{2,5}C - (K_{2,5}K_{3,4} + K_{2,3}K_{4,5})B)}{K_{2,3}K_{4,5}K_{5,1} + K_{2,5}K_{3,4}K_{5,1} - K_{4,5}A - K_{2,5}C} > 0,$$

we can know that species S_1, S_2, S_3, S_4 and S_5 will not become extinct if they exist at the beginning.

Acknowledgments

The authors thank anonymous referees for their helpful comments.

Author Contributions

Conceived and designed the experiments: YK QP MH. Performed the experiments: YK. Analyzed the data: YK XW MH. Contributed reagents/materials/analysis tools: YK. Wrote the paper: YK XW.

References

1. Czaran T. L., Hoekstra R. F., and Pagie L., Proc. Natl Acad. Sci. USA 99, 786(2002). PMID: [11792831](#)
2. Kerr B., Riley M. A., Feldman M. W., and Bohannan B. J. M., Nature 418, 171(2002). PMID: [12110887](#)
3. Reichenbach T., Mobilia M., and Frey E., Nature 448, 1046(2007). PMID: [17728757](#)
4. Reichenbach T., Mobilia M., and Frey E., Phys. Rev. E, 74 (5), 051907(2006).
5. Claussen J. C., and Traulsen A., Physical Review Letters 100 (5), 058104 (2008). PMID: [18352437](#)

6. Jackson J. B. C., and Buss L., *Proc. Natl Acad. Sci. USA* 72, 5160(1975). PMID: [16592298](#)
7. Taylor D. R., and Aarssen L. W., *Am. Nat.* 136, 305(1990).
8. Silvertown J., Holtier S., Johnson J., and Dale P., *J. Ecol.* 80, 527(1992).
9. Durrett R., and Levin S., *Theor. Popul. Biol.* 53, 30(1998). PMID: [9500909](#)
10. Lankau R. A., and Strauss S. Y., *Science* 317, 1561(2007). PMID: [17872447](#)
11. Cameron D. D., White A., and Antonovics J., *J. Ecol.* 97, 1311(2009).
12. Durrett R., and Levin S., *J. Theor. Biol.* 185, 165(1997). PMID: [9344720](#)
13. Kirkup B. C., and Riley M.A., *Nature* 428, 412(2004). PMID: [15042087](#)
14. Neumann G. F., and Jetschke G., *Biosystems* 99, 155(2010). doi: [10.1016/j.biosystems.2009.10.007](#) PMID: [19883727](#)
15. Nahum J. R., Harding B. N., and Kerr B., *Proc. Natl Acad. Sci. USA* 108, 10831(2011). doi: [10.1073/pnas.1100296108](#) PMID: [21690371](#)
16. Sinervo B., and Lively C. M., *Nature* 380, 240(1996).
17. Gilg O., Hanski I., and Sittler B., *Science* 302, 866(2003). PMID: [14593179](#)
18. Guill C., Drossel B., Just W., and Carmack E., *J. Theor. Biol.* 276, 16(2011). doi: [10.1016/j.jtbi.2011.01.036](#) PMID: [21291894](#)
19. Berlow E. L. et al., *J. Anim. Ecol.* 73, 585(2004).
20. Stouffer D. B., Sales-Pardo M., Sizer M. I., and Bascompte J., *Science* 335, 1489(2012). doi: [10.1126/science.1216556](#) PMID: [22442483](#)
21. Avelino P., Bazeia D., Menezes J., and de Oliveira B., *Physics Letters A* 378 (4), 393 (2014).
22. Dobrinevski A., Alava M., Reichenbach T., and Frey E., *Phys. Rev. E* 89 (1), 012721 (2014).
23. Durney C. H., Case S. O., Pleimling M., and Zia R. K. P., *Phys. Rev. E* 83 (5), 051108 (2011).
24. Feng S. S. and Qiang C. C., *Physica A* 392 (19), 4675 (2013).
25. Intoy B. and Pleimling M., *J. Stat. Mech.-Theory Exp.*, P08011 (2013).
26. Kang Y. B., Pan Q. H., Wang X. T., and He M. F., *Physica A* 392 (11), 2652 (2013).
27. Vukov J., Szolnoki A., and Szabó G., *Phys. Rev. E* 88 (2), 022123 (2013).
28. Szolnoki A., Mobilia M., Jiang L. L., zczesny B., Rucklidge A. M., and Perc M., *Journal of the Royal Society Interface* 11(100), 20140735 (2014).
29. Cheng H.Y., Yao N., Huang Z. G., Park J., Do Y., and Lai Y. C., *Scientific Reports* 4, 7486(2014) doi: [10.1038/srep07486](#) PMID: [25501627](#)
30. Knebel J., Kruger T., Weber M. F., and Frey E., *Physical Review Letters* 110 (16), 168106 (2013). PMID: [23679644](#)
31. Laird R. A. and Schamp B. S., *J. Theor. Biol.* 256 (1), 90 (2009). doi: [10.1016/j.jtbi.2008.09.017](#) PMID: [18948120](#)
32. Li Y., Dong L., and Yang G., *Physica A* 391 (1–2), 125 (2012).
33. Sun G. Q., Wu Z. Y., and Wang Z., *Nonlinear Dyn.* 83, 811 (2016).
34. Li L., *Applied Mathematics and Computation* 258, 342 (2015).
35. Sun G. Q., Zhang J., Song L. P., Jin Z., and Li B. L., *Applied Mathematics and Computation* 218, 11151 (2012).
36. Sun G. Q., *Nonlinear Dyn.* 69, 1097 (2012).
37. Sun G. Q., Jin Z., Li L., and Haque M., *Nonlinear Dyn.* 69, 1631 (2012).
38. Sun G. Q., Wang S. L., Ren Q., Jin Z., and Wu Y. P., *Scientific Reports* 5, 11246 (2015). doi: [10.1038/srep11246](#) PMID: [26084812](#)
39. Sun G. Q., Chakraborty A., Liu Q. X., Jin Z., Anderson K. E., and Li B. L., *Commun. Nonlinear Sci. Numer. Simulat.* 19, 1507 (2014).
40. Li L., Jin Z., and Li J., *Applied Mathematical Modelling* 40, 4765 (2016).
41. Imhof L. A., Fudenberg D., and Nowak M. A., *J. Theor. Biol.* 247(3), 574(2007). PMID: [17481667](#)
42. Levin S. A., *Ecology* 73(6), 1943(1992).
43. Szabó G., Szolnoki A., and Sznajder G. A., *Phys. Rev. E* 76(5), 051921(2007).
44. Szabó G., Szolnoki A., and Borsos I., *Phys. Rev. E* 77(4), 041919(2008).