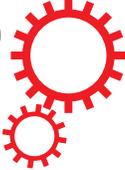


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Emergence of unusual coexistence states in cyclic game systems

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Evolutionary games of cyclic competitions have been extensively studied to gain insights into one of the most fundamental phenomena in nature: biodiversity that seems to be excluded by the principle of natural selection. The Rock-Paper-Scissors (RPS) game of three species and its extensions [e.g., the Rock-Paper-Scissors-Lizard-Spock (RPSLS) game] are paradigmatic models in this field. In all previous studies, the intrinsic symmetry associated with cyclic competitions imposes a limitation on the resulting coexistence states, leading to only selective types of such states. We investigate the effect of nonuniform intraspecific competitions on coexistence and find that a wider spectrum of coexistence states can emerge and persist. This surprising finding is substantiated using three classes of cyclic game models through stability analysis, Monte Carlo simulations and continuous spatiotemporal dynamical evolution from partial differential equations. Our finding indicates that intraspecific competitions or alternative symmetry-breaking mechanisms can promote biodiversity to a broader extent than previously thought.

Fundamental to species coexistence and biodiversity are competitions. In ecosystems there are two types of competitions: interspecific (competitions among individuals from different species) and intraspecific (competitions among individuals in the same species), where both types can either promote or hinder species coexistence^{1,2}. The purpose of this paper is to demonstrate, through a systematic study of several models of cyclic evolutionary game, that intraspecific competitions can induce unusual states of coexistence that have not been reported previously. Intraspecific competitions may thus be more fundamental to biodiversity than previously thought.

A natural and typical mechanism for interspecific competitions is predator-prey interaction, while intraspecific competitions occur because individuals in the same species compete for essential life-sustaining resources such as food, water, light, and opposite sex. A well known type of intraspecific competitions is cannibalism or intraspecific predation^{3–10}, which can occur with high likelihood especially when there is lack of sufficient resources. Such competitions can also occur when individuals fight each other for mating opportunities, which were observed for side-blotched lizards in California¹¹. In the past decade there were studies of the effect of intraspecific competitions on biodiversity^{12–16}, with results such as the experimental finding that the competitions tend to drive disruptive selection¹², enhanced host survival through intraspecific competition between co-infecting parasite strains¹³, and directional selection of certain fish species^{15,16}.

To understand coexistence and biodiversity, the approach of mathematical modeling has proven to be useful, providing fundamental insights into the various mechanisms underlying species coexistence at both the macroscopic, population^{17–19} and the microscopic, individual competition levels^{20–23}. Historically, the theoretical approach began with mathematically modeling growth and competitions through dynamical equations at the population level^{17–19}. In the past fifteen years or so, microscopic models at the level of individual interactions were extensively studied based on the mathematical paradigm of evolutionary games^{24–53}. A milestone result^{22,26} is the elucidation of the role of species mobility in coexistence, which traditionally had been regarded as detrimental to coexistence. In particular, utilizing the framework of three cyclic competing species, the rock-paper-scissors (RPS) model, the authors^{22,26} demonstrated robust coexistence in the weak mobility regime, providing a resolution to the paradox that macroscopic models exclude coexistence of mobile species but, in realistic ecological processes ranging from bacteria run and tumble to animal migration, coexistence is ubiquitous. The basic dynamical structure supporting the coexistence of mobile species was identified to be spiral wave patterns that emerge and evolve with time in the physical space²², which are robust against noise²⁶. Other issues that have

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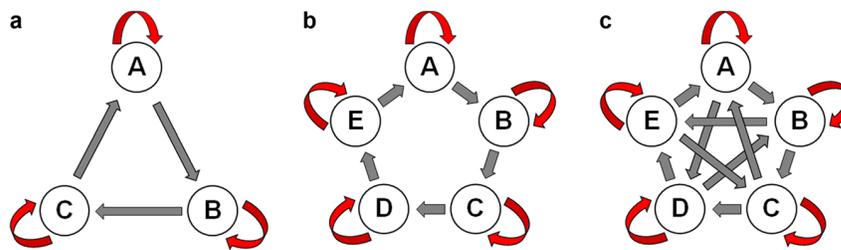


Figure 1. Cyclic games with intraspecific competitions. (a) Rock-paper-scissors (RPS) game of three species, (b) Extended Rock-Paper-Scissors (ERPS) game of five species, and (c) Rock-Paper-Scissors-Lizard-Spock (RPSLS) game of five species. Straight and looped arrows indicate interspecific and intraspecific competitions, respectively.

been investigated include the stability of spatial patterns^{24, 29, 39, 52, 54–57}, the role of conservation laws^{27, 44}, pairwise and group-level interactions⁵³, basins of the coexistence states^{30, 31}, and the effects of a wide array of behaviors/quantities on coexistence such as long range migration^{38, 45}, uniform intraspecific competition³², local habitat suitability⁴⁶, multi-strategy competition⁴⁹, inhomogeneous reaction rates^{28, 33, 40, 47, 48}, epidemic spreading³⁴, and spatial extent and population size^{25, 36, 41}. While most of these works were for three cyclic competing species, there were studies extending the model to arbitrary number of species^{42, 43, 53} and addressing the role of competition at the mesoscopic (i.e., group) level in coexistence⁵². Here extinction means no coexistence and only one surviving species in the system.

In previous works, a well established result is that only a certain type of coexistence states can exist. For example, in a system of three cyclically competing species (RPS game), the only coexistence state is one that involves all three species: it is not possible for a state of two coexisting species^{22, 26} to be stable. Likewise, in a cyclic system of five species, there are two distinct coexistence states with either three or five species - there cannot be coexistence states with two or four species⁵². The reason for the selective coexistence states lies in the intrinsic symmetry of the system, as the competing species are at the same footing. Intuitively, symmetry breaking can possibly lead to more diverse coexistence states. The purpose of this paper is to demonstrate and establish that realistic intraspecific competitions that generically break the intrinsic symmetry of cyclic competitions, can lead to *all possible coexisting states*. In particular, in the real world the degree of intraspecific competition in general depends on the particular species. To describe symmetry-breaking in a concrete way, we use a parameter, e.g., the rate of intraspecific competition. The rate can then be nonuniform for different species, which can have a significant effect on the game dynamics^{33, 58–61}. At the microscopic level, the species are thus no longer on the equal footing - effectively introducing symmetry breaking into the system. As a result, coexisting states without a global symmetry at the macroscopic level can arise. We establish this striking result through extensive computations and mathematical analyses of cyclically competing systems with different number of species.

Results

Models and mathematical representations. To investigate the dynamical evolutions of cyclically competing species in the presence of intraspecific competitions, we study three game systems: the classic RPS model, the extended RPS (ERPS) model of five species, and the rock-paper-scissors-lizard-spock (RPSLS) model. The dynamical interacting rules of the three models are shown in Fig. 1. At the microscopic level, each model can be described by evolutionary dynamics on a lattice system, while at the macroscopic level the model can be approximated by a set of ordinary differential equations (ODEs). In addition, partial differential equations (PDEs) can be used to study the spatiotemporal evolution of the population densities.

For convenience, we employ a square lattice with periodic boundary conditions to host a cyclic game system at the microscopic level, where an individual occupies a lattice site. Given the interspecific competition rate σ , species reproduction rate μ , intraspecific competition rate p , and movement rate ε , interactions among the individuals can be described by

$$XY \xrightarrow{\sigma} X\emptyset, \quad X\emptyset \xrightarrow{\mu} XX, \quad XX \xrightarrow{p} X\emptyset, \quad XZ \xrightarrow{\varepsilon} ZX, \quad (1)$$

where X and Y represent two cyclically interacting species, \emptyset denotes an empty site, and Z stands for either an individual from the same species or an empty site, and the quantity ε is defined to be $\varepsilon \equiv 2MN$ with M being the individual mobility parameter and N being the total number of individuals. In the evolutionary game system, each site can be occupied by an individual from one of the species or left empty. At each time step, a randomly selected individual can compete, reproduce, or move into one of its nearest neighbors at random, provided that the corresponding interaction rule as specified in Eq. (1) is satisfied.

Under the mean field approximation where the population size is large: $N \rightarrow \infty$, the system can be described by the rate equations governing the time evolution of the species densities (ODEs). Let $a(t)$, $b(t)$, and $c(t)$ be the densities of the three species A , B , and C at time t , respectively. The RPS game model can be described by

$$\begin{aligned}
 \frac{da}{dt} &= a \left[\mu(1 - \rho) - \sigma c - \frac{p_a}{2} a \right], \\
 \frac{db}{dt} &= b \left[\mu(1 - \rho) - \sigma a - \frac{p_b}{2} b \right], \\
 \frac{dc}{dt} &= c \left[\mu(1 - \rho) - \sigma b - \frac{p_c}{2} c \right],
 \end{aligned} \tag{2}$$

where $\rho(t) \equiv a(t) + b(t) + c(t)$ is the total density of the three species. In each equation, the first and second terms describe reproduction of a species at rate μ and a decrease in the species density by invasion at rate σ , respectively. The third term represents the decrease in the density due to intraspecific competition of rates p_a , p_b , or p_c for species A, B and C, respectively, where the factor 1/2 associated with the rate accounts for the two-way interactions between two individuals in the same species. (ODE models for ERPS and RPSLS games are provided in Supplementary Information).

The ODE model ignores the effects of the spatial domain in which the interactions occur. To take into account the spatial dimension, a PDE model can be derived. In particular, consider a square domain of linear size L with periodic boundary conditions, where $L^2 = N$. We normalize the domain to the unit square so that the distance between two nearest neighbors is $\delta x = 1/\sqrt{N} = (1/L)$. The densities of subpopulations A, B, and C at time t and site $\mathbf{x} = (x_1, x_2)$ are denoted as $a(\mathbf{x}, t)$, $b(\mathbf{x}, t)$, and $c(\mathbf{x}, t)$, respectively. For interspecific and intraspecific competitions as well as reproduction, the dynamical equations for these quantities only involve neighbors located at $\mathbf{x} \pm \delta \mathbf{x} \cdot \mathbf{e}_i$, where $\{\mathbf{e}_i\}_{i=1,2}$ are the base vectors of the lattice. For the RPS game, we obtain the following evolutionary equations:

$$\begin{aligned}
 \frac{\partial a(\mathbf{x}, t)}{\partial t} &= M \Delta a(\mathbf{x}, t) + \mu a(\mathbf{x}, t) [1 - \rho(\mathbf{x}, t)] - \sigma a(\mathbf{x}, t) c(\mathbf{x}, t) - \frac{p_a}{2} a(\mathbf{x}, t) a(\mathbf{x}, t), \\
 \frac{\partial b(\mathbf{x}, t)}{\partial t} &= M \Delta b(\mathbf{x}, t) + \mu b(\mathbf{x}, t) [1 - \rho(\mathbf{x}, t)] - \sigma b(\mathbf{x}, t) a(\mathbf{x}, t) - \frac{p_b}{2} b(\mathbf{x}, t) b(\mathbf{x}, t), \\
 \frac{\partial c(\mathbf{x}, t)}{\partial t} &= M \Delta c(\mathbf{x}, t) + \mu c(\mathbf{x}, t) [1 - \rho(\mathbf{x}, t)] - \sigma b(\mathbf{x}, t) c(\mathbf{x}, t) - \frac{p_c}{2} c(\mathbf{x}, t) c(\mathbf{x}, t).
 \end{aligned} \tag{3}$$

where $M = \frac{\epsilon}{2} (1/\sqrt{N})^2$. (The corresponding PDEs for ERPS and RPSLS games are provided in Supplementary Information).

To be concrete, in this paper we fix the rates of interspecific competition and reproduction to be $\sigma = 1$ and $\mu = 1$, respectively.

Coexistence states in the RPS system. Figure 2 illustrates the possible coexistence states in the RPS system, where the middle column represents a state in which two species coexist - a previously unknown coexistence state. Specifically, a stability analysis of the corresponding ODE system with respect to systematic changes in an intraspecific competition parameter, say p_a , with fixed $p_b = 1$ and $p_c = 0.5$, reveals the following phenomena. Firstly, for weak intraspecific competition, i.e., $0 < p_a \leq 1.5$, coexistence is physically not possible due to the existence of a heteroclinic cycle, where only one species can survive. Secondly, for moderate intraspecific competition, i.e., $1.5 < p_a \leq 4$, for each species reproduction and death are counter-balanced, so all three species can coexist, as indicated by the left column in Fig. 2. Thirdly, for stronger intraspecific competition, i.e., $p_a > 4$, the new coexistence state of two species emerges, as indicated by the middle column in Fig. 2. The striking consequence is that, in this case, the nature of the interaction between the two surviving species has become the predator-prey type as a result of the balance between prey's reproduction and predator's death from competitions among its own individuals. In the limit of infinitely strong intraspecific competition, i.e., $p_a \rightarrow \infty$, the predator becomes extinct, leaving the prey as the only surviving species, as shown in the right column of Fig. 2. Figure 3(a) presents a bifurcation diagram of these behaviors (see Methods for more details).

The spatial patterns associated with distinct coexisting states can be revealed by numerical solutions of the lattice and PDE models, Eqs (1) and (3), respectively. Figure 2(c–e) show, for $M = 10^{-3}$, nine representative snapshots of the spatial patterns in the long time regime for different values of p_a , where the three species are denoted by red, blue, and yellow, respectively. Specifically, the three columns (from left to right) are associated with $p_a = 2.5, 5.2$ and 100 , respectively, the two top rows [Fig. 2(c,d)] are from lattice models of size $L = 100 \times 100$ and 500×500 , respectively, and the bottom row is from the PDE model. We see that, all possible coexistence states can occur and, as the intraspecific competition parameter is increased, physical coexistence states for which the number of survival species is in the order $1 \rightarrow 3 \rightarrow 2 \rightarrow 1$ emerge, which is consistent with the results from the bifurcation analysis of the ODE model. Further, we find that the thresholds between different stable phases from lattice simulations are consistent with those from the bifurcation analysis of the ODE model, as supported by a calculation of the survival probability P_{surv} from 100 sampled parameter values (see Fig. S9 in Supplementary Information). The middle column shows the patterns of the coexistence state of two species in the spatial domain, which has not been observed previously in the cyclic game of three species. Previous studies also revealed that the coexistence state of three species is supported by spiral waves in the domain^{22,26}. In general, spiral waves can be stable, unstable or convectively unstable even in the absence of intraspecific competitions^{54–56}. However, with intraspecific competition induced symmetry breaking at the microscopic level, various coexistence states can arise but no spiral wave patterns can form.

Coexistence states in the ERPS system. There are five competing species in the ERPS system, as shown in Fig. 1(b). To be concrete, we consider a fixed set of parameter values: $p_a = 1.9$, $p_b = 2$, $p_d = 1.3$, and $p_e = 0.7$. A

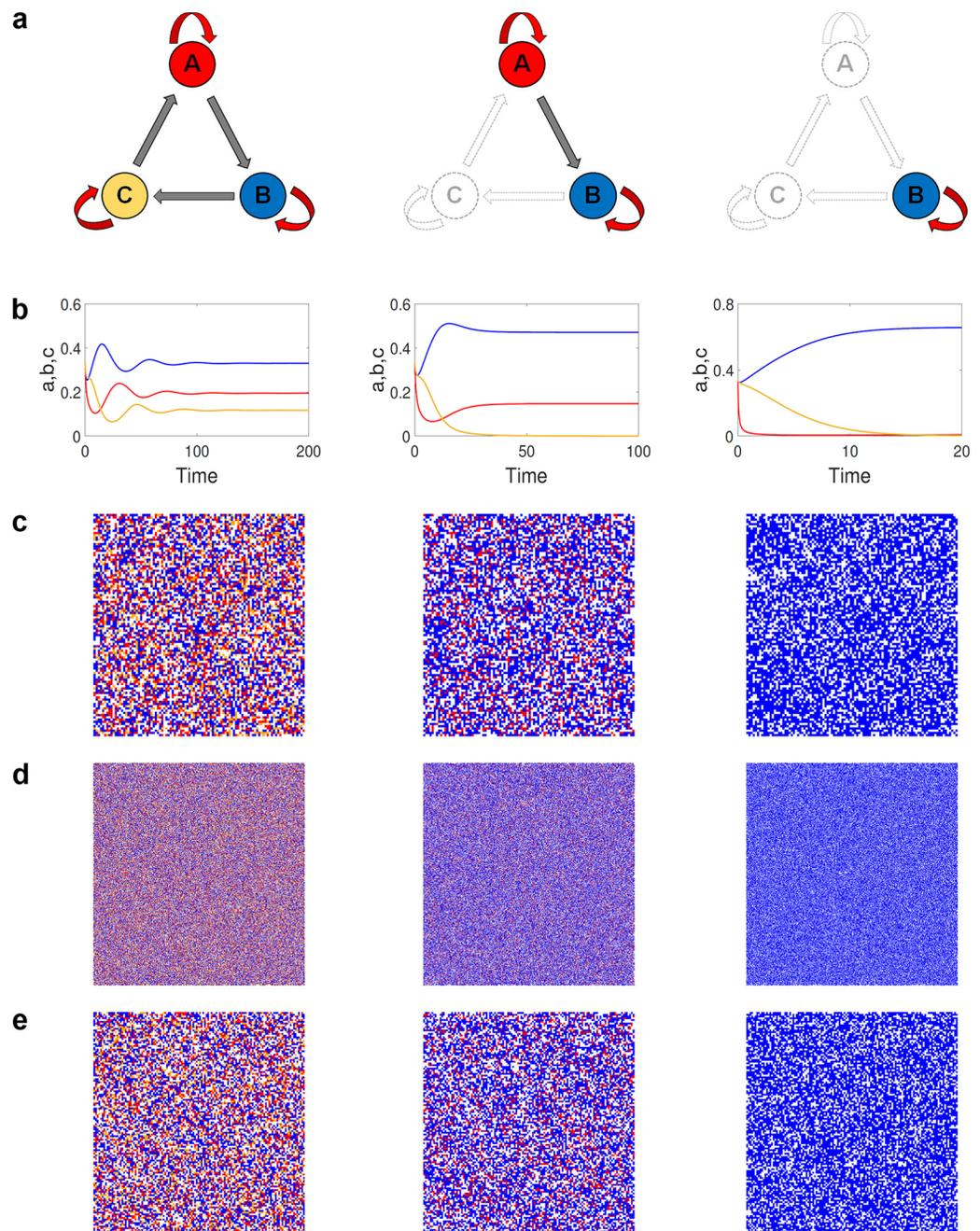


Figure 2. All possible coexistence states in RPS game. Red, blue and yellow colors indicate different species and blank denotes empty sites. (a) Three different types of surviving species. The left column corresponds to $p_a = 2.5$, where (b) shows the density evolution from the ODE model, (c) and (d) present typical snapshots obtained from Monte Carlo simulations of lattice size $N = 100 \times 100$ and 500×500 , respectively, and (e) is a snapshot obtained from the PDE model. The middle and right columns are for $p_a = 5.2$ and $p_a = 100$, respectively. Other parameters are $p_b = 1.0$ and $p_c = 0.5$.

bifurcation analysis of the underlying ODE model (Supplementary Information) leads to the following results on the role of intraspecific competition in coexistence. Firstly, for weak intraspecific competition, i.e., $0 \leq p_c < 2.6$, mathematically all species can coexist but small perturbations can lead to extinction, physically excluding coexistence. Secondly, for a moderate level of intraspecific competition, i.e., $2.6 \leq p_c < 5.6$, all species can physically coexist. Thirdly, in the regime of strong intraspecific competition, i.e., $5.6 < p_c < 5.8$, coexistence states of four species can emerge, breaking the cyclic symmetry. Fourthly, for stronger intraspecific competition, i.e., $p_c \geq 5.8$, three species can coexist, exhibiting a predator-prey relation. For $p_c \rightarrow \infty$, the predator populations diminish and only two species can coexist. Figure 3(b) presents a bifurcation diagram of these behaviors.

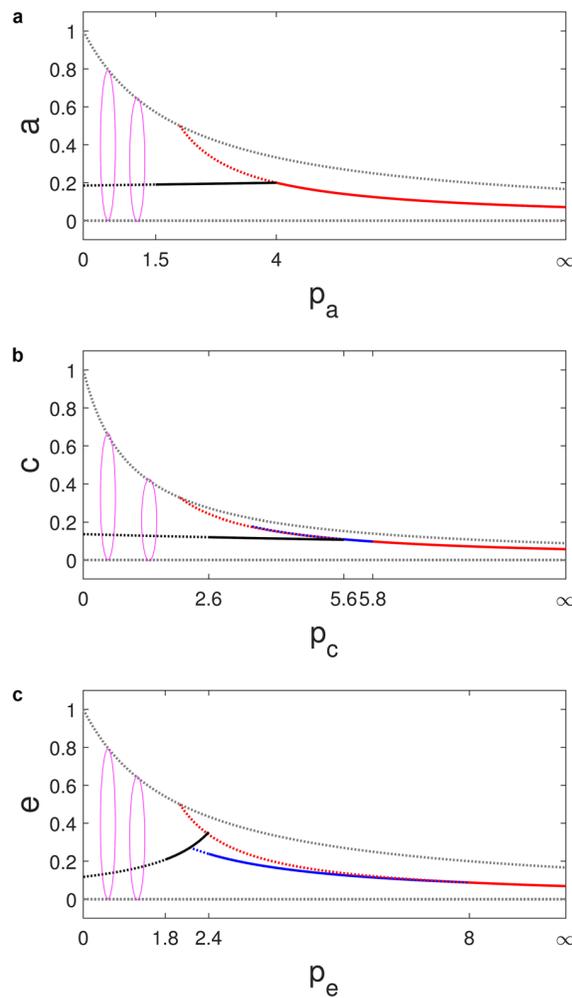


Figure 3. Bifurcation with intraspecific parameter. Solid lines and ellipses indicate stable fixed points and heteroclinic cycles, respectively, and dots are for unstable fixed points. Different fixed points are distinguished by colors. **(a)** For the RPS game, the survival states of three and two species (black and red lines), respectively. **(b)** For the ERPS game, black, blue and red lines indicate the survival states of five, four, and three species, respectively. **(c)** For the RPSLS game, black, blue and red lines specify the survival states of five, four and three species, respectively.

The emergence of all possible coexistence states, especially the unusual states of three and four coexisting species, can be substantiated by resorting to the lattice and PDE models (see Supplementary Information for the PDE model of the ERPS system). To be concrete, we set the simulation parameters to be $p_a = 1.9$, $p_b = 2$, $p_d = 1.3$, $p_e = 0.7$, and $M = 10^{-3}$. Figure 4(c–e) show fifteen snapshots of the spatial patterns in the long time regime from the lattice and PDE models for a number of different values of p_c , where the five species are denoted by red, blue, green, yellow and pink, respectively. The panels are organized into rows and columns, where columns 1–4 (from left to right) are associated with $p_c = 3.3, 5.65, 6.5$ and 100 , and column 5 is for $p_c = 100$ but with a different parameter setting ($p_a = 1.9$, $p_b = 2$, $p_d = 0.01$, and $p_e = 0.7$). The two top rows [Fig. 4(c,d)] are the results from lattices of size $L = 100 \times 100$, 500×500 , respectively, and the bottom row represents the results from the PDE model. These results are consistent with those from the stability analysis of the corresponding ODE system in that coexistence states of all possible numbers of species can occur. The most striking phenomenon is the coexistence of four and three species (corresponding to the second and third columns, respectively), which have not been reported previously for the ERPS system. Similar to the RPS system, with intraspecific competitions the coexistence states are not supported by spiral wave patterns in the spatial domain.

Coexistence states in the RPSLS system. For the five-species RPSLS system, for a representative set of fixed parameter values, e.g., $p_a = 0.3$, $p_b = 1.1$, $p_c = 2.5$, and $p_d = 0.7$, but varying p_e , a stability analysis reveals the following phenomena. Firstly, in the regime of weak intraspecific competition, i.e., $0 \leq p_e < 1.8$, coexistence is physically not possible. Secondly, for $1.8 \leq p_e < 2.4$, coexistence of all five species is physically realizable and robust. Thirdly, for $2.4 \leq p_e < 8$, coexistence of five species is no longer possible. Instead, coexistence states of four species can emerge, breaking the cyclic symmetry. Fourthly, for $p_e \geq 8$, only three species, which do not

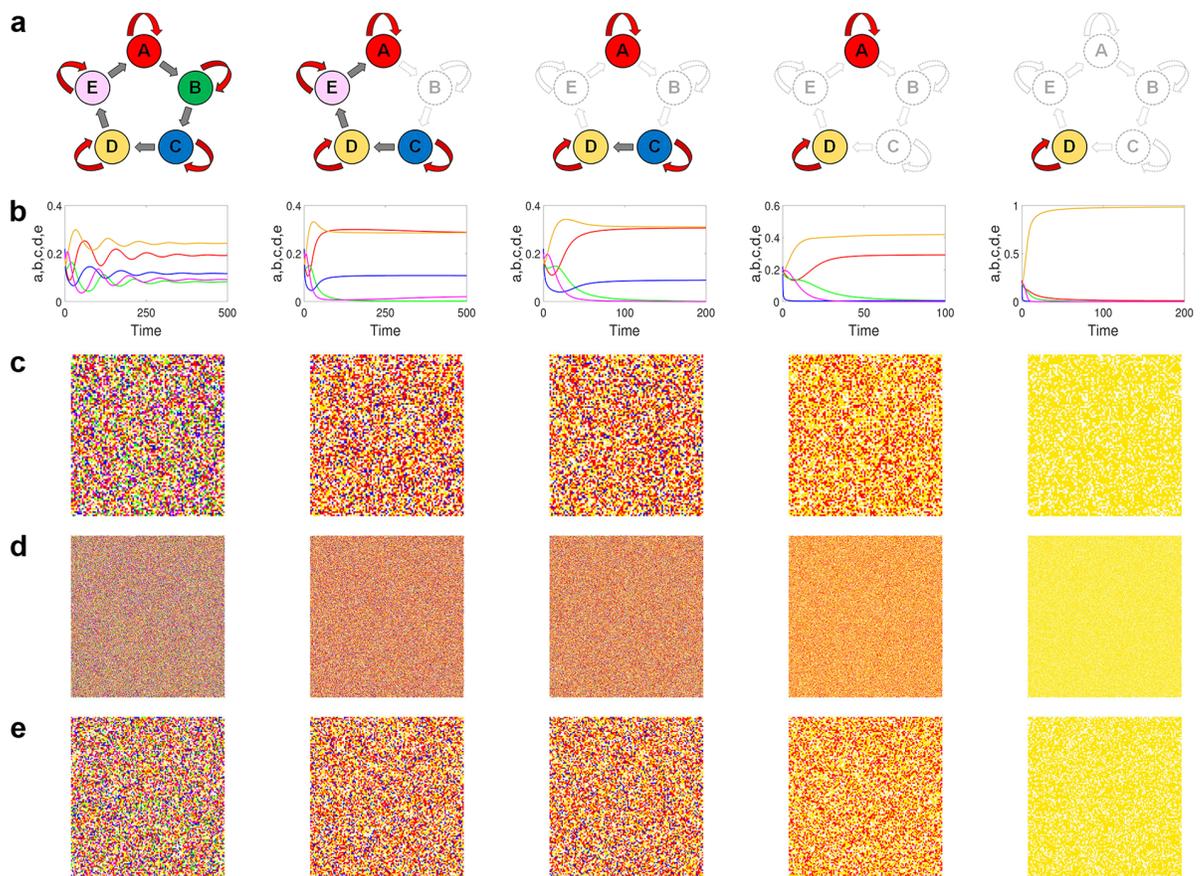


Figure 4. Coexistence states in ERPS game. (a) Five different types of surviving species, where each color denotes a different species (blank for empty site). The four columns from left correspond to four different values of the intraspecific competition rate of one species: $p_c = 3.3, 5.65, 6.5$ and 100 , respectively, with fixed parameters $p_a = 1.9, p_b = 2.0, p_d = 1.3$, and $p_e = 0.7$. For example, in the left most column, (b) is the density evolution from the ODE model, (c,d) are typical snapshots obtained from Monte Carlo simulations of lattice size $N = 100 \times 100$ and 500×500 , respectively, and (e) is a snapshot obtained from the PDE model. The right most column is for $p_a = 1.9, p_b = 2.0, p_c = 100, p_d = 0.01$, and $p_e = 0.7$.

exhibit a sub-cyclic structure, can coexist and, for $p_e \rightarrow \infty$, two of the three species can survive in a predator-prey relation. Figure 3(c) presents a bifurcation diagram of these behaviors. Detailed simulations from the lattice and PDE (Supplementary Information) models give consistent results. For example, for $p_a = 0.3, p_b = 1.1, p_c = 2.5$, and $p_d = 0.7$, various coexistence states can emerge for different values of p_e , as shown by the spatial patterns in Fig. 5(c–e). The results shown in the second and fourth columns, which indicate the coexistence states of four and two species, are surprising as such states have not been uncovered previously in the study of RPSLS system⁵². We also find that, associated with the coexistence of three species [c.f., Fig. 5(a)], there is absence of any cyclic interaction structure among the three survived species. This is in fact a *non-sub-cyclic interacting structure* which, to our knowledge, has not been reported previously in the studies of interspecific interaction models^{52,62}. For the ten distinct cases of three survived species among five, the coexistence states with such a non-sub-cyclic structure are stable. Interestingly, the conventional coexistence states with a sub-cyclic structure among the three surviving species are unstable (See Supplementary Information for more details). It is also apparent that, dynamically, the coexistence states are not supported by spiral wave patterns.

Role of intraspecific competition in promoting diverse coexistence states - a qualitative understanding.

To understand the effect of intraspecific competition on coexistence qualitatively, we investigate the population change for each species i as a result of interspecific and intraspecific competitions as well as reproduction at time t , denoted as $C_i(t), I_i(t)$ and $R_i(t)$ (scaled by the lattice size N), respectively. From the fact that the populations are determined by the balance between reproduction and competition, we find it useful to define two quantities: $H_i(t) = R_i(t) - C_i(t)$ and $S_i(t) = R_i(t) - C_i(t) - I_i(t)$. We then have $H_i(t) - S_i(t) = I_i(t) \geq 0$ and the population at time t can be written as $P_i(t) = P_i^0 + \int_0^t S_i(k) dk$ for a given initial population P_i^0 . For $S_i(t) > 0$, species i can survive as its population tends to increase with time, which will cause a decrease in the population of the next species in the cycle (prey of species i) as a result of interspecific competitions, leading to possible extinction. For $S_i(t) < 0$, the population of species i decreases and possibly becomes extinct. These simple observations imply that,

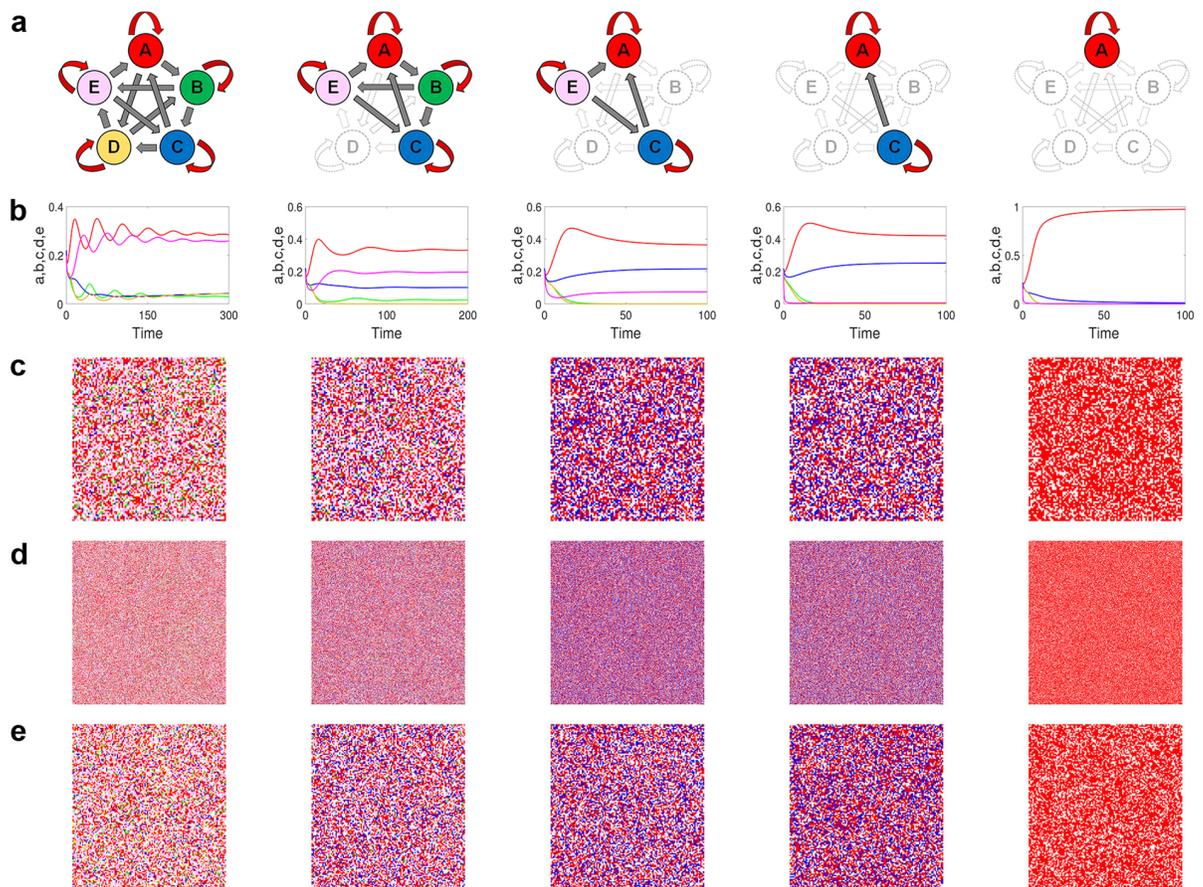


Figure 5. Coexistence states in RPSLS game. (a) Five different types of surviving species, where each color denotes a different species (blank for empty site). The four columns from left correspond to four different values of the intraspecific competition rate of one species: $p_e = 2.2, 3.3, 9.3$ and 100 , respectively, with fixed parameters $p_a = 0.3, p_b = 1.1, p_c = 2.5$ and $p_d = 0.7$. For example, in the left most column, (b) is the density evolution from the ODE model, (c,d) are typical snapshots obtained from Monte Carlo simulations of lattice size $N = 100 \times 100$ and 500×500 , respectively, and (e) is a snapshot obtained from the PDE model. The right most column is for $p_a = 0.01, p_b = 1.1, p_c = 2.5, p_d = 0.7$, and $p_e = 100$.

in order for multiple species to survive, $S_i(t)$ must fluctuate about zero. Equivalently, for surviving species i , its population fluctuations can be described by a normal diffusion process: $\langle S_i^2(t) \rangle \sim t$.

For the case of the coexistence of three species in the RPS system, Fig. 6(a) shows the time evolution of $H_i(t)$ and $S_i(t)$. We observe that $H_i(t) > 0$ but $S_i(t)$ fluctuates about zero, which indicates that, without intraspecific competitions, the corresponding populations tend to increase with time due to $H_i(t) > 0$. However, intraspecific competition can reduce the populations, because $S_i \approx 0$. This implies that a possible balance between the increasing and decreasing trends can be attained, stabilizing the populations. For the case of species extinction [Fig. 6(b,c)], we find that H_i can be positive initially but becomes negative due to the decrease in the reproduction as a result of strong intraspecific competitions.

For the cyclic system of three species ($A \rightarrow B \rightarrow C \rightarrow A$), we note that each pair of species constitutes a predator-prey system. To examine the process leading to the coexistence of two species, we assume a decrease in the population of predator (A) from its initial population due to strong intraspecific competitions, which will immediately reduce the interspecific competition with its prey (B). As a result, the prey population can increase due to reproduction. The change in the population of species (B) will in turn enhance the interspecific competition with its prey (C), leading to a decrease in its population and possibly to its extinction. This chain of interactions indicates that intraspecific competition of a species can have a dramatic effect on the populations of other interacting species, potentially generating a distinct equilibrium state. To provide theoretical support, we identify the critical level of intraspecific competition leading to qualitative changes in the species populations through a mathematical analysis of the existence and the stability conditions of the equilibrium states listed in Table 1 (see Methods and Supplementary Information).

In the three species system, the coexistence state of two species is characteristic of that of a predator-prey system. Intuitively, the classic Lotka-Volterra model can be used to describe such a situation, where the populations can exhibit periodic oscillations with time (or a limit cycle in the phase space). We find that, however, in the presence of intraspecific competitions, the populations of the coexisting species do not exhibit periodic oscillations

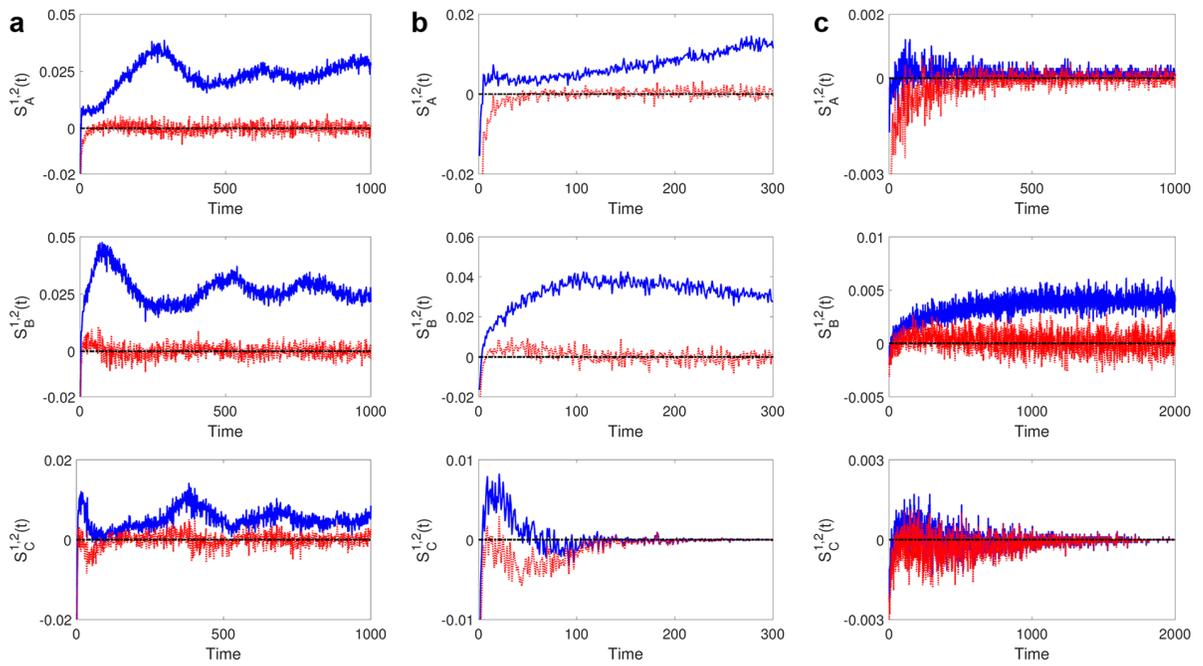


Figure 6. Qualitative indicator of effect of intraspecific competition on coexistence in RPS game. Each column shows the quantities H_i (blue) and S_i (red) for each species, where the corresponding coexistence states are indicated by three, two and one from left to right. (a) There is a gap between blue and red quantities all time. (b) The gap between the two quantities of a species (bottom panel) is reduced and finally disappears. The top and bottom panels of the third column in (c) show the collapsed gap between the two quantities.

Species	AB	AC	BC
Fixed point	$w_1(p_b, p_a - 2, 0)$	$w_2(p_c - 2, 0, p_a)$	$w_3(0, p_c, p_b - 2)$
λ_i	$w_1(p_a(p_b - 2) + 4)/2$	$w_2(p_c(p_a - 2) + 4)/2$	$w_3(p_b(p_c - 2) + 4)/2$
	$-w_1 p_b(p_a - 2)/2$	$-w_2 p_a(p_c - 2)/2$	$-w_3 p_c(p_b - 2)/2$
	-1	-1	-1
Existence	$p_a > 2$	$p_a > 0$	$p_b > 2$
	$p_b > 0$	$p_c > 2$	$p_c > 0$
	$p_b > \frac{4 - 2p_a}{p_a + 2}$	$p_a > \frac{4 - 2p_c}{p_c + 2}$	$p_c > \frac{4 - 2p_b}{p_b + 2}$
Stable Condition	$p_a(p_b - 2) + 4 < 0$	$p_c(p_a - 2) + 4 < 0$	$p_b(p_c - 2) + 4 < 0$
	$p_a > \frac{4}{2 - p_b}, p_b < 2$	$p_c > \frac{4}{2 - p_a}, p_a < 2$	$p_b > \frac{4}{2 - p_c}, p_c < 2$

Table 1. Existence and stability conditions of fixed points of type p_2 in the RPS game.

but steady states, as shown in Fig. 2(b). Thus, intraspecific competitions can either enhance coexistence and induce diverse coexistence states, or break the equilibrium and lead to extinction.

Discussion

In the classic three- or five-species cyclic games, the species are on the equal footing in the sense that no particular species is superior or inferior to any other species. This intrinsic symmetry imposes a restriction on the survival or coexistence states of the system. For example, for the classic RPS game, either only one species survives as a result of interspecific interactions in which the end result is the disappearance of such competitions, or all three species can sustain and coexist^{20–23}. For this reason the coexistence state of two species has never been reported before in the literature. Likewise, for the five-species RPSLS game, the known coexistence states contain a sole surviving species, three species, or all five species⁵². It is conceivable that, when the intrinsic symmetry among the competing species is broken, more diverse types of coexistence states can emerge.

Nonuniform intraspecific competitions represent one mechanism that can break the symmetry: they put the species on unequal footings. For example, if competitions among individuals in a species are stronger than those in another species, the former requires more resources to reproduce in order to survive and is therefore effectively “inferior” to the latter. As a result, a predator-prey type of behavior can emerge on the macroscopic scale where intraspecific competitions associated with the predator are stronger than those with the prey to reach a new equilibrium state in which the two surviving species are no longer on equal footing. Mathematically, it is not necessary

for such a state to possess any intrinsic symmetry. The consequence is that coexistence states involving any number of species (insofar the number is less than or equal to the total number of species in the system) can arise.

The contributions of this paper are mathematical analyses, physical understanding, and comprehensive numerical tests that symmetry breaking can lead to more diverse coexistence states than previously reported. To accomplish this goal, we systematically studied three classes of cyclic game systems with either three or five species, subject to nonuniform, species dependent, intraspecific competitions. For each system, we focus on the asymptotic dynamical states (i.e., the coexistence states) of the system utilizing three approaches: ODE based stability analysis, microscopic Monte-Carlo simulation of the lattice model, and spatiotemporal evolution of the corresponding PDE model. A detailed bifurcation analysis of the ODE model reveals that, as the strength of the intraspecific competition for one species is systematically varied (while keeping the intraspecific competition strengths for the other species fixed), coexistence states of any number of species can arise in different parameter regimes. The occurrence of these states is further supported by both lattice and PDE simulations. A distinct feature is that the coexistence states here are not associated with any spiral wave patterns that were previously established as the underlying spatiotemporal dynamical structure supporting the coexistence of multiple species in cyclic game systems^{22,26}. Our findings suggest that symmetric breaking with nonuniform intraspecific competitions across the species may be more beneficial to biodiversity.

Methods

Numerical methods. All PDE models are solved by the standard spectral method and lattice simulations are of the Monte Carlo type. Lattice sizes vary from 100×100 to 500×500 .

Stability analysis of RPS game. In the classic RPS game in the absence of intraspecific competitions (i.e., $p_i = 0$), there are two possible states: one in which all three species coexist and another with only one surviving species. In the presence of intraspecific competitions, a new type of states in which two species coexist can arise, which can be seen by finding the fixed points of the ODE model, Eq. (2), and analyzing their stabilities. The first type of fixed points, denoted by \mathbf{p}_1 , correspond to an extinction state:

$$\left(\frac{2}{2 + p_a}, 0, 0 \right), \left(0, \frac{2}{2 + p_b}, 0 \right), \left(0, 0, \frac{2}{2 + p_c} \right). \quad (4)$$

The second type \mathbf{p}_2 is for states in which two species coexist and one species is extinct:

$$w_1(p_b, p_a - 2, 0), \quad (5)$$

$$w_2(p_c - 2, 0, p_a), \quad (6)$$

$$w_3(0, p_c, p_b - 2), \quad (7)$$

where $w_1 = 2/(p_a p_b + 2(p_a + p_b) - 4)$, $w_2 = 2/(p_a p_c + 2(p_a + p_c) - 4)$, and $w_3 = 2/(p_b p_c + 2(p_b + p_c) - 4)$. The existence and stability conditions of type \mathbf{p}_2 fixed points are summarized in Table 1. The last type \mathbf{p}_3 corresponds to the state in which all three species survive, i.e., (a^*, b^*, c^*) , where

$$a^* = 2(p_b(p_c - 2) + 4)/\Gamma, \quad b^* = 2(p_c(p_a - 2) + 4)/\Gamma, \quad c^* = 2(p_a(p_b - 2) + 4)/\Gamma, \quad (8)$$

and $\Gamma = p_a p_b p_c + 8 + 2[p_a p_b + p_b p_c + p_c p_a - 2(p_a + p_b + p_c) + 12]$. For a more detailed analysis of stability and existence of fixed points, see Supplementary Information.

To assess the stabilities of these different types of fixed points in a concrete way, we fix $(p_b, p_c) = (1, 0.5)$ and vary the parameter p_a . For $p_a \geq 0$, there are three fixed points of type \mathbf{p}_1 and one fixed point of type \mathbf{p}_3 . However, for $p_a \geq 2$, only one fixed point of type \mathbf{p}_2 [Eq. (5)] exists. The three fixed points of type \mathbf{p}_1 are saddles for $p_a \geq 0$. While for $0 < p_a \leq 1.5$ all fixed points are unstable, and there is an asymptotically stable heteroclinic cycle constituting three heteroclinic orbits connecting any two saddle fixed points (all of the \mathbf{p}_1 type). Since the cycle is arbitrarily close to the saddle fixed points, a small perturbation can cause a trajectory to diverge from the cycle, leading to extinction. For $1.5 < p_a \leq 4$, the fixed point of the type \mathbf{p}_3 [Eq. (8)] becomes stable, in which all species coexist. We note that, for $p_a \geq 2$, fixed points of the type \mathbf{p}_2 [Eq. (5)] are created and are unstable. For $p_a > 4$, the fixed points given by Eqs (5) and (8) become stable and unstable, respectively, indicating the emergence of the coexistence state of two species. In this case, the fixed point given by Eq. (5) is globally stable. As p_a is increased further, this fixed point approaches an extinction state:

$$\frac{2}{p_a p_b + 2(p_a + p_b) - 4} (p_b, p_a - 2, 0) \rightarrow (0, 2/3, 0) \text{ as } p_a \rightarrow \infty.$$

Figure 3(a) presents a bifurcation diagram of these behaviors.

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Author Contributions

J.P., B.J. and Y.D. devised the research project. J.P. performed numerical simulations. J.P., B.J., Y.D. and Y.C.L. analyzed the results and wrote the paper.

Additional Information

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Supplementary Information for

Emergence of unusual coexistence states in cyclic game systems

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Contents

1	Stability analysis of rock-paper-scissors system	2
1.1	Uniform intraspecific competitions	2
1.2	Nonuniform intraspecific competitions	2
2	Extended rock-paper-scissors system	5
2.1	ODE based stability analysis	5
2.2	PDE model	7
3	Rock-paper-scissors-lizard-spock system	7
3.1	ODE based Stability analysis	8
3.2	PDE model	10
4	Supplementary Tables	11
5	Supplementary References	12
6	Supplementary Figures	13

1 Stability analysis of rock-paper-scissors system

1.1 Uniform intraspecific competitions

For uniform intraspecific competitions: $p_a = p_b = p_c = p$, the ODE model of the RPS system is given by

$$\begin{aligned}\frac{da}{dt} &= a \left[\mu(1 - \rho) - \sigma c - \frac{p}{2}a \right], \\ \frac{db}{dt} &= b \left[\mu(1 - \rho) - \sigma a - \frac{p}{2}b \right], \\ \frac{dc}{dt} &= c \left[\mu(1 - \rho) - \sigma b - \frac{p}{2}c \right].\end{aligned}\tag{S1}$$

There are three types of possible states: extinction (type \mathbf{p}_1), coexistence of two species (type \mathbf{p}_2), and coexistence of all three species (type \mathbf{p}_3). The corresponding fixed point solutions are listed in Supplementary Tab. S1. To be concrete, we set $\sigma = 1$ and $\mu = 1$. The system has three fixed points of type \mathbf{p}_1 , which are unstable for $p > 0$. For the \mathbf{p}_2 type, three fixed points exist for $p > 2$ and $p^2 + 4p - 4 > 0$ but they are unstable with a positive eigenvalue $\lambda_2 > 0$, as listed in Supplementary Tab. S1. For \mathbf{p}_3 , an unstable fixed point exists for $p < 1$ but it becomes stable for $p > 1$.

For $0 < p < 1$, the three fixed points of type \mathbf{p}_1 constitute a heteroclinic cycle, whose stability can be evaluated [S1]. Since they have identical eigenvalues, the corresponding eigenvalue ratios are identical as well

$$V_i = -\lambda_s^1 / \lambda_u = \frac{2-p}{p}.\tag{S2}$$

The product V of the ratios is

$$V = \prod_{i=1}^3 V_i = \left(\frac{2-p}{p} \right)^3 > 1.\tag{S3}$$

The heteroclinic cycle signifies coexistence but it is physically unstable as random perturbations will land the system into one of the extinction states. For $p \geq 1$, a typical trajectory converges to the stable fixed point \mathbf{p}_3 . Supplementary Fig. S1 shows a bifurcation diagram and representative trajectories of the system.

1.2 Nonuniform intraspecific competitions

With nonuniform intraspecific competitions, the system becomes

$$\begin{aligned}\frac{da}{dt} &= a \left[(1 - \rho) - c - \frac{p_a}{2}a \right], \\ \frac{db}{dt} &= b \left[(1 - \rho) - a - \frac{p_b}{2}b \right], \\ \frac{dc}{dt} &= c \left[(1 - \rho) - b - \frac{p_c}{2}c \right].\end{aligned}\tag{S4}$$

There are three types of fixed points:

$$\mathbf{p}_1 : \left(\frac{2}{2+p_a}, 0, 0 \right), \left(0, \frac{2}{2+p_b}, 0 \right), \left(0, 0, \frac{2}{2+p_c} \right),\tag{S5}$$

$$\mathbf{p}_2 : w_4(p_b, p_a - 2, 0), w_5(p_c - 2, 0, p_a), w_6(0, p_c, p_b - 2),\tag{S6}$$

$$\mathbf{p}_3 : (a^*, b^*, c^*),\tag{S7}$$

where

$$\begin{aligned}
w_4 &= 2/(p_a p_b + 2(p_a + p_b) - 4), \\
w_5 &= 2/(p_a p_c + 2(p_a + p_c) - 4), \\
w_6 &= 2/(p_b p_c + 2(p_b + p_c) - 4), \\
a^* &= 2(p_b(p_c - 2) + 4)/\Gamma, \\
b^* &= 2(p_c(p_a - 2) + 4)/\Gamma, \\
c^* &= 2(p_a(p_b - 2) + 4)/\Gamma, \\
\Gamma &= p_a p_b p_c + 2(p_a p_b + p_b p_c + p_c p_a) - 4(p_a + p_b + p_c) + 32.
\end{aligned}$$

The three fixed points of type \mathbf{p}_1 are unstable:

$$\lambda_1 = -1, \quad \lambda_2 = \frac{p_a - 2}{2 + p_a}, \quad \lambda_3 = \frac{p_a}{2 + p_a}.$$

We summarize the existence and stability conditions of the three fixed points of type \mathbf{p}_2 in Supplementary Tab. S2.

To study the effect of nonuniform intraspecific competitions on coexistence, we consider three concrete scenarios: (1) fixing the values of the intraspecific competition rate for two species and varying the third, (2) fixing one rate and varying the remaining two, and (3) fixing the sum of the three rates ($p_1 + p_2 + p_3 = \alpha$) and varying the value of the sum. For the first scenario, for fixed $p_a = p_b$ and value of p_c open, we find coexistence states. In particular, for $p_a = p_b < 2$, as p_c is increased, global attractors such as stable heteroclinic cycles can arise, as well as coexisting state \mathbf{p}_3 of all three species and the two-species coexistence state \mathbf{p}_2 , as shown in Supplementary Fig. S2. In this case, the existence range and the stabilities of the fixed points of types \mathbf{p}_2 and \mathbf{p}_3 depend on the value of p_c . If we decrease the value of $p_a = p_b$, the existence interval of the fixed point \mathbf{p}_3 as a globally stable attractor strictly increases, but that of the stable heteroclinic cycle decreases. For sufficiently large values of p_c , a fixed point of type \mathbf{p}_2 exists and is stable. That is, two species can coexist, which is not possible when the intraspecific competitions are uniform. For $p_a = p_b > 2$, coexistence of all three species is stable for any value of p_c .

For the second scenario, we fix the value of p_a and vary p_b and p_c . Supplementary Fig. S3 shows the emergence and disappearance of various survival states. Specifically, we observe a decrease in the parameter region for a stable heteroclinic cycle and one of fixed points of type \mathbf{p}_2 (AC), but the region for the survival state of species B and C does not change, as detailed in Supplementary Tab. S2. That is, fixed points of type \mathbf{p}_2 have emerged. We also observe that for an increased value of p_a , varying p_b and p_c can expand the parameter regions for the fixed point \mathbf{p}_3 . In general, nonuniform intraspecific competitions can induce new survival states and/or disappearance of previous survival states.

For the third scenario, we vary $p_a, p_b, p_c \geq 0$ while keeping their sum α fixed. Supplementary Fig. S4 shows the various survival states in the 2-simplex plane for several α values ranging from 0.6 to 60. We use different colors to denote different states: a stable heteroclinic cycle (white), three different fixed points of type \mathbf{p}_2 (red, blue and yellow for coexisting species AB, AC and BC , respectively), and the fixed point \mathbf{p}_3 for stable coexistence of all species (black). Specifically, for $\alpha < 2$, a stable heteroclinic cycle constituting three saddle fixed points of type \mathbf{p}_1 is the global attractor of the system, whereas fixed points of type \mathbf{p}_2 do not exist and the fixed point \mathbf{p}_3 exists but it is unstable. For $\alpha > 2$, a dramatic change in the survival states occurs: depending on the rates of the intraspecific competitions, a coexisting state of two species emerges, which has not been observed in previous studies of the RPS system. In general, the coexistence states \mathbf{p}_2

and \mathbf{p}_3 begin to emerge from the three vertices of the 2-simplex plane $p_a + p_b + p_c = \alpha$. As α is increased, the parameter region of \mathbf{p}_3 expands toward the center of the 2-simplex from each of the three vertices and merge into a larger region, as can be seen in the top two rows in Supplementary Fig. S4. The two-species coexistence states \mathbf{p}_2 are born from the vertices of the 2-simplex and expand following its edges. From the bottom two rows in Supplementary Fig. S4, we see that, for a sufficiently large value of α , the interior of the 2-simplex is fully covered by the two distinct coexistence states \mathbf{p}_2 and \mathbf{p}_3 . For $\alpha \geq \alpha_h \approx 3.7$, the stable heteroclinic cycle no longer exists. As the value of α is increased further, the ratio of the area of three basins for \mathbf{p}_2 to the total area of the 2-simplex plane increases until when $\alpha \leq \alpha_c \approx 5.9$ and then decreases for $\alpha > \alpha_c$.

We numerically calculate the existence boundaries for each attractor for $\alpha = 5$ with parameters p_a , p_b and p_c from the 2-simplex plane, as shown in Supplementary Fig. S5. Exploiting the existence condition of the fixed points of type \mathbf{p}_2 as listed in Supplementary Tab. S2, we can derive each boundary curve analytically. For example, setting $p_b = 4/(2 - p_c)$, we can obtain the parameter boundary of the coexisting state of two species (B and C - yellow region in Supplementary Fig. S5). In particular, we have

$$p_a + \frac{4}{2 - p_c} + p_c = \alpha \quad (\alpha > 2),$$

which implies

$$p_a = \alpha - \frac{4}{2 - p_c} - p_c = \alpha - \frac{p_c^2 - 2p_c - 4}{p_c - 2}.$$

To further study the difference in the characteristics between coexistence of two and three species, we study the dynamical behaviors of the system for two parameter settings located above and below the boundary in Supplementary Fig. S5: (1) $(p_a, p_b, p_c) = (1.7, 2.8, 0.5)$ for \mathbf{p}_2 and (2) $(p_a, p_b, p_c) = (1.7, 2.7, 0.6)$ for \mathbf{p}_3 . We see that species A becomes extinct under parameter setting (1), while it survives under setting (2). To understand this behavior, we note that, for setting (1), although the intraspecific competitions within A and B are stronger than that of species C , it is A that becomes extinct. Supplementary Fig. S6 shows the densities of the three species from the lattice simulation, and we obtain essentially the same patterns from the corresponding PDE model (data not shown). How interspecific and intraspecific competitions as well as reproduction affect the densities can also be seen from Supplementary Fig. S6.

A possible dynamical process leading to the coexistence of two species is as follows. A decrease in the population of species B subject to strong intraspecific competitions can be beneficial to its prey (species C), leading to an increase in the prey population. As a result, species A will be at a disadvantage because it is the prey of C . It can happen that reproduction of A is not sufficient to sustain the population decrease due to interactions with C , leading to extinction of A . That is, an increase in self-competition within one species can cause the extinction of other species.

For parameter setting (2), species A survives even if its population is much reduced, as shown in Supplementary Fig. S7. This behavior is quite different from that under setting (1), indicating the emergence of a critical borderline between the two settings. This may have implications for population control. For example, under setting (2), intraspecific competitions within species B are stronger than those within the other two species, leading to an increase in their populations, which in turn causes their predators' populations to increase.

2 Extended rock-paper-scissors system

For the five-species, extended rock-paper-scissors (ERPS) system, in the absence of intraspecific competitions, there are three possible states [S2]: the coexistence state of all five species, states in which two non-interacting species survive, and extinction states of only one surviving species. As demonstrated in the main text, with nonuniform intraspecific competitions all possible coexistence states can arise.

2.1 ODE based stability analysis

The ODE model of the ERPS system is

$$\begin{aligned}
 \frac{da}{dt} &= a \left[\mu(1 - \rho) - \sigma e - \frac{p_a}{2} a \right], \\
 \frac{db}{dt} &= b \left[\mu(1 - \rho) - \sigma a - \frac{p_b}{2} b \right], \\
 \frac{dc}{dt} &= c \left[\mu(1 - \rho) - \sigma b - \frac{p_c}{2} c \right], \\
 \frac{dd}{dt} &= d \left[\mu(1 - \rho) - \sigma c - \frac{p_d}{2} d \right], \\
 \frac{de}{dt} &= e \left[\mu(1 - \rho) - \sigma d - \frac{p_e}{2} e \right].
 \end{aligned} \tag{S8}$$

To be concrete, we fix $\sigma = \mu = 1$. There are five types of fixed points. The first type, denoted by \mathbf{q}_1 , corresponds to various extinction states:

$$\begin{aligned}
 &\left(\frac{2}{2 + p_a}, 0, 0, 0, 0 \right), \left(0, \frac{2}{2 + p_b}, 0, 0, 0 \right), \left(0, 0, \frac{2}{2 + p_c}, 0, 0 \right), \\
 &\left(0, 0, 0, \frac{2}{2 + p_d}, 0 \right), \left(0, 0, 0, 0, \frac{2}{2 + p_e} \right).
 \end{aligned} \tag{S9}$$

The second type \mathbf{q}_2 specifies states in which only two species coexist. Five of such fixed points are

$$\frac{2}{p_a p_c + 2(p_a + p_c)} (p_c, 0, p_a, 0, 0), \tag{S10}$$

$$\frac{2}{p_a p_d + 2(p_a + p_d)} (p_d, 0, 0, p_a, 0), \tag{S11}$$

$$\frac{2}{p_b p_d + 2(p_b + p_d)} (0, p_d, 0, p_b, 0), \tag{S12}$$

$$\frac{2}{p_b p_e + 2(p_b + p_e)} (0, p_e, 0, 0, p_b), \tag{S13}$$

$$\frac{2}{p_c p_e + 2(p_c + p_e)} (0, 0, p_e, 0, p_c), \tag{S14}$$

which are unstable. The third type \mathbf{q}_3 signifies the coexistence state of three species. The possibly stable fixed points of this type are

$$\frac{2(p_b p_d, p_d(p_a - 2), 0, p_a p_b, 0)}{p_a p_b p_d + 2(p_a p_b + p_a p_d + p_b p_d) - 4p_d}, \quad (\text{S15})$$

$$\frac{2(p_c p_d, 0, p_a p_d, p_a(p_c - 2), 0)}{p_a p_c p_d + 2(p_a p_c + p_a p_d + p_c p_d) - 4p_a}, \quad (\text{S16})$$

$$\frac{2(p_c(p_e - 2), 0, p_a p_e, 0, p_a p_c)}{p_a p_c p_e + 2(p_a p_c + p_a p_e + p_c p_e) - 4p_c}, \quad (\text{S17})$$

$$\frac{2(0, p_c p_e, p_e(p_b - 2), 0, p_b p_c)}{p_b p_c p_e + 2(p_b p_c + p_b p_e + p_c p_e) - 4p_e}, \quad (\text{S18})$$

$$\frac{2(0, p_d p_e, 0, p_b p_e, p_b(p_d - 2))}{p_b p_d p_e + 2(p_b p_d + p_b p_e + p_d p_e) - 4p_b}. \quad (\text{S19})$$

The fourth type \mathbf{q}_4 describes the state in which four species coexist and only one species is extinct. For example, one such fixed point, denoted as $(a^*, 0, c^*, d^*, e^*)$, is given by

$$a^* = \frac{2(p_c(p_d(p_e - 2) + 4) - 8)}{\Sigma_4}, \quad c^* = \frac{p_a p_d p_e}{\Sigma_4}, \quad d^* = \frac{2p_a p_e(p_c - 2)}{\Sigma_4}, \quad (\text{S20})$$

$$e^* = \frac{2p_a(p_c(p_d - 2) + 4)}{\Sigma_4},$$

where

$$\Sigma_4 = p_a p_c p_d p_e + 2(p_a p_c p_d + p_a p_c p_e + p_a p_d p_e + p_c p_d p_e) - 4(p_a p_c + p_a p_e + p_c p_d) + 8(p_a + p_c) - 16.$$

The last type \mathbf{q}_5 corresponds to the state in which all five species survive, i.e., $(a^*, b^*, c^*, d^*, e^*)$, where

$$a^* = \frac{2(p_b p_c p_d p_e - 2p_b p_c p_d + 4p_b p_c - 8p_b + 16)}{\Sigma_5},$$

$$b^* = \frac{2(p_a p_c p_d p_e - 2p_c p_d p_e + 4p_c p_d - 8p_c + 16)}{\Sigma_5},$$

$$c^* = \frac{2(p_a p_b p_d p_e - 2p_a p_d p_e + 4p_d p_e - 8p_d + 16)}{\Sigma_5}, \quad (\text{S21})$$

$$d^* = \frac{2(p_a p_b p_c p_e - 2p_a p_b p_e + 4p_a p_e - 8p_e + 16)}{\Sigma_5},$$

$$e^* = \frac{2(p_a p_b p_c p_d - 2p_a p_b p_c + 4p_a p_b - 8p_a + 16)}{\Sigma_5},$$

and

$$\begin{aligned} \Sigma_5 &= p_a p_b p_c p_d p_e + 2(p_a p_b p_c p_d + p_a p_b p_c p_e + p_a p_b p_d p_e + p_a p_c p_d p_e + p_b p_c p_d p_e) \\ &- 4(p_a p_b p_c + p_a p_b p_e + p_b p_c p_d + p_a p_d p_e + p_c p_d p_e) + 8(p_a p_b + p_b p_c + p_a p_e + p_c p_d + p_d p_e) \\ &- 16(p_a + p_b + p_c + p_d + p_e) + 192. \end{aligned}$$

To assess the stabilities of the fixed points, we fix $(p_a, p_b, p_d, p_e) = (1.9, 2, 1.3, 0.7)$ and vary the parameter p_c . For $p_c > 0$, there are fixed points of types \mathbf{q}_1 and \mathbf{q}_2 which are unstable. For $p_c > 2$, the fixed point (S16) of type \mathbf{q}_3 can exist and the fixed point (S20) of type \mathbf{q}_4 emerges for $3.5 \leq p_c < 5.8$. For $0 < p_c < 2.6$,

although the fixed points of types \mathbf{q}_1 , \mathbf{q}_2 , \mathbf{q}_3 and \mathbf{q}_5 exist, only the cycles consisting of the heteroclinic orbits connecting saddle fixed points of type \mathbf{q}_2 are numerically observable. For $2.6 \leq p_c < 5.6$, the fixed point \mathbf{q}_5 becomes stable in which all species coexist. However, this fixed point no longer exists for $p_c \geq 5.6$. For $p_c \geq 5.8$, the fixed points (S20) disappear. For $p_c \geq 5.8$, the three-species coexisting fixed points (S16) become stable and approach the two-species fixed points (S11) as $p_c \rightarrow \infty$. Thus, for large values of p_c , the coexistence states of two species are numerically observable, as shown in the bifurcation diagram and a spatial snapshot (Figs. 3 and 4, respectively) in the main text. In general, as the intraspecific competition parameter is increased, a variety of coexistence states can emerge.

2.2 PDE model

Taking into account the spatial dimension, we obtain a set of PDEs:

$$\begin{aligned}
\frac{\partial a(\mathbf{x}, t)}{\partial t} &= M\Delta a(\mathbf{x}, t) + \mu a(\mathbf{x}, t)[1 - \rho(\mathbf{x}, t)] - \sigma e(\mathbf{x}, t)a(\mathbf{x}, t) - \frac{p_a}{2}a(\mathbf{x}, t)a(\mathbf{x}, t), \\
\frac{\partial b(\mathbf{x}, t)}{\partial t} &= M\Delta b(\mathbf{x}, t) + \mu b(\mathbf{x}, t)[1 - \rho(\mathbf{x}, t)] - \sigma a(\mathbf{x}, t)b(\mathbf{x}, t) - \frac{p_b}{2}b(\mathbf{x}, t)b(\mathbf{x}, t), \\
\frac{\partial c(\mathbf{x}, t)}{\partial t} &= M\Delta c(\mathbf{x}, t) + \mu c(\mathbf{x}, t)[1 - \rho(\mathbf{x}, t)] - \sigma b(\mathbf{x}, t)c(\mathbf{x}, t) - \frac{p_c}{2}c(\mathbf{x}, t)c(\mathbf{x}, t), \\
\frac{\partial d(\mathbf{x}, t)}{\partial t} &= M\Delta d(\mathbf{x}, t) + \mu d(\mathbf{x}, t)[1 - \rho(\mathbf{x}, t)] - \sigma c(\mathbf{x}, t)d(\mathbf{x}, t) - \frac{p_d}{2}d(\mathbf{x}, t)d(\mathbf{x}, t), \\
\frac{\partial e(\mathbf{x}, t)}{\partial t} &= M\Delta e(\mathbf{x}, t) + \mu e(\mathbf{x}, t)[1 - \rho(\mathbf{x}, t)] - \sigma d(\mathbf{x}, t)e(\mathbf{x}, t) - \frac{p_e}{2}e(\mathbf{x}, t)e(\mathbf{x}, t),
\end{aligned} \tag{S22}$$

where $a(\mathbf{x}, t)$, $b(\mathbf{x}, t)$, $c(\mathbf{x}, t)$, $d(\mathbf{x}, t)$, and $e(\mathbf{x}, t)$ denote the densities of the five species at site $\mathbf{x} = (x_1, x_2)$ and time t on a square domain with periodic boundary conditions.

3 Rock-paper-scissors-lizard-spock system

For the rock-paper-scissors-lizard-spock (RPSLS) system of five species, in the absence of intraspecific competitions, three types of distinct dynamical states can arise [S3] [S4]: the coexistence state of all five species, states in which three species having a sub-cyclic interacting structure coexist, and extinction states of only one surviving species. In the main text, we demonstrate that intraspecific competitions can induce coexistence states of any possible number of surviving species.

3.1 ODE based Stability analysis

Similar to the ERPS system, the coupled ODE model for the RPSLS system is

$$\begin{aligned}
\frac{da}{dt} &= a \left[\mu(1 - \rho) - \sigma e - \sigma c - \frac{p_a}{2} a \right], \\
\frac{db}{dt} &= b \left[\mu(1 - \rho) - \sigma a - \sigma d - \frac{p_b}{2} b \right], \\
\frac{dc}{dt} &= c \left[\mu(1 - \rho) - \sigma b - \sigma e - \frac{p_c}{2} c \right], \\
\frac{dd}{dt} &= d \left[\mu(1 - \rho) - \sigma c - \sigma a - \frac{p_d}{2} d \right], \\
\frac{de}{dt} &= e \left[\mu(1 - \rho) - \sigma d - \sigma b - \frac{p_e}{2} e \right].
\end{aligned} \tag{S23}$$

There are different types of fixed points with different numbers of surviving species. For $\sigma = \mu = 1$, fixed points of different types are listed below.

The first type, denoted as \mathbf{r}_1 , describes the extinction states:

$$\begin{aligned}
&\left(\frac{2}{2 + p_a}, 0, 0, 0, 0 \right), \left(0, \frac{2}{2 + p_b}, 0, 0, 0 \right), \left(0, 0, \frac{2}{2 + p_c}, 0, 0 \right), \\
&\left(0, 0, 0, \frac{2}{2 + p_d}, 0 \right), \left(0, 0, 0, 0, \frac{2}{2 + p_e} \right).
\end{aligned} \tag{S24}$$

The second type \mathbf{r}_2 represents states in which only two species survive. For example, two of the ten possible fixed points are

$$\frac{2(p_c - 2, 0, p_a, 0, 0)}{p_a p_c + 2(p_a + p_c) - 4}, \text{ and } \frac{2(0, 0, p_d, p_c - 2, 0)}{p_c p_d + 2(p_c + p_d) - 4}, \tag{S25}$$

which are unstable. The third type, denoted by \mathbf{r}_3 , corresponds to three coexisting species. In this case, there are ten such fixed points, three of which are

$$\frac{2(0, p_c(p_d - 2) + 4, p_d(p_b - 2) + 4, p_b(p_c - 2) + 4, 0)}{\Delta_{31}}, \tag{S26}$$

$$\frac{2(0, 0, p_d(p_e - 2) + 4, p_e(p_c - 2) + 4, p_c(p_d - 2) + 4)}{\Delta_{32}}, \tag{S27}$$

and

$$\frac{2((p_c - 2)(p_e - 2), 0, p_a(p_e - 2), 0, p_a p_c)}{\Delta_{33}}, \tag{S28}$$

where

$$\begin{aligned}
\Delta_{31} &= p_b p_c p_d + 2(p_b p_c + p_b p_d + p_c p_d) - 4(p_b + p_c + p_d) + 32, \\
\Delta_{32} &= p_c p_d p_e + 2(p_c p_d + p_c p_e + p_d p_e) - 4(p_d + p_e + p_c) + 32, \\
\Delta_{33} &= p_a p_c p_e + 2(p_a p_c + p_a p_e + p_c p_e) - 4(p_a + p_c + p_e) + 8.
\end{aligned}$$

Fixed points such as those in (S28) have a *non-sub-cyclic structure* and can be stable in certain parameter ranges, while other five points including (S26)-(S27) with a sub-cyclic structure are always unstable as the eigenvalues of the underlying Jacobian matrices under the existence condition are positive. For example, for

the fixed point (S26), we have

$$\begin{aligned}
\lambda_1 &= -1, \quad \lambda_2 = \frac{(p_b - 2)(p_c(p_d - 2) + 4)}{\Delta_{31}}, \quad \lambda_3 = \frac{p_d(p_b(p_c - 2) + 4)}{\Delta_{31}}, \\
\lambda_{4,5} &= [128 - 80(p_c + p_d) + 8(p_c^2 + p_d^2) + 56p_cp_d - 8p_cp_d(p_c + p_d) + 2p_c^2p_d^2 \\
&\quad - p_b(p_c(-56 + 52p_d - 6p_d^2) + 8(10 - 7p_d + p_d^2) + p_c^2(8 - 6p_d + p_d^2)) \\
&\quad - p_b^2(-2(p_d - 2)^2 + p_c(8 - 6p_d + p_d^2) + p_c^2(-2 + p_d + p_d^2)) \\
&\quad \pm \{(\Delta_{31})^2(p_b^2(2 - p_c + p_d)^2 + (p_d - 2)(4p_cp_d - 2) + p_c^2(p_d - 2) + 4(p_d + 6)) \\
&\quad - 2p_b(p_c^2(p_d - 2) + p_c(8 - 6p_d + p_d^2) + 2(-4 + 4p_d + p_d^2))\}^{\frac{1}{2}} / (\Delta_{31})^2,
\end{aligned} \tag{S29}$$

and λ_3 is positive because of the inequality $p_b(p_c - 2) + 4 > 0$. An illustration of the classification of the structures of the fixed points of type \mathbf{r}_3 is presented in Supplementary Fig. S8.

The fourth fixed-point type \mathbf{r}_4 corresponds to states in which four species coexist and one species is extinct. One such fixed point, for example $(a^*, b^*, c^*, 0, e^*)$, is given by

$$\begin{aligned}
a^* &= \frac{2(p_b p_c p_e + 4(p_b + p_c + p_e) - 2p_b(p_c + p_e) - 8)}{\Delta_4} \\
b^* &= \frac{2(p_a p_c p_e + 4(p_c + p_e) - 2p_c p_e - 8)}{\Delta_4} \\
c^* &= \frac{2(p_e - 2)(p_a(p_b - 2) + 4)}{\Delta_4}, \quad e^* = \frac{2p_c(p_a(p_b - 2) + 4)}{\Delta_4},
\end{aligned} \tag{S30}$$

where

$$\begin{aligned}
\Delta_4 &= p_a p_b p_c p_e + 2(p_a p_b p_c + p_a p_b p_e + p_a p_c p_e + p_b p_c p_e) \\
&\quad - 4(p_a p_b + p_a p_c + p_b p_c + p_a p_e + p_b p_e + p_c p_e) + 32(p_c + p_e) + 8(p_a + p_b) - 64.
\end{aligned}$$

The last fixed-point type, \mathbf{r}_5 , characterizes the coexistence state of all five species, which is given by $(a^*, b^*, c^*, d^*, e^*)/\Delta_5$, where

$$\begin{aligned}
a^* &= 2\{16 - 8(p_b + p_c + p_d) + 4(p_b p_c + p_b p_d + p_c p_d + p_d p_e) - 2(p_b p_c p_d + p_b p_d p_e) + p_b p_c p_d p_e\}, \\
b^* &= 2\{16 - 8(p_c + p_d + p_e) + 4(p_c p_d + p_a p_e + p_c p_e + p_d p_e) - 2(p_a p_c p_e + p_c p_d p_e) + p_a p_c p_d p_e\}, \\
c^* &= 2\{16 - 8(p_a + p_d + p_e) + 4(p_a p_b + p_a p_d + p_a p_e + p_d p_e) - 2(p_a p_b p_d + p_a p_d p_e) + p_a p_b p_d p_e\}, \\
d^* &= 2\{16 - 8(p_a + p_b + p_e) + 4(p_a p_b + p_b p_c + p_a p_e + p_b p_e) - 2(p_a p_b p_e + p_b p_c p_e) + p_a p_b p_c p_e\}, \\
e^* &= 2\{16 - 8(p_a + p_b + p_c) + 4(p_a p_b + p_a p_c + p_b p_c + p_c p_d) - 2(p_a p_b p_c + p_a p_c p_d) + p_a p_b p_c p_d\},
\end{aligned} \tag{S31}$$

and

$$\begin{aligned}
\Delta_5 &= p_a p_b p_c p_d p_e + 2(p_a p_b p_c p_d + p_a p_b p_c p_e + p_a p_b p_d p_e + p_a p_c p_d p_e + p_b p_c p_d p_e) \\
&\quad - 4(p_a p_b p_c + p_a p_b p_d + p_a p_c p_d + p_b p_c p_d + p_a p_b p_e + p_a p_c p_e + p_b p_c p_e + p_a p_d p_e + p_b p_d p_e + p_c p_d p_e) \\
&\quad + 32(p_a p_b + p_b p_c + p_c p_d + p_a p_e + p_d p_e) + 8(p_a p_c + p_a p_d + p_b p_d + p_b p_e + p_c p_e) \\
&\quad - 64(p_a + p_b + p_c + p_d + p_e) + 224.
\end{aligned}$$

To analyze the stabilities of all the fixed points, we set $(p_a, p_b, p_c, p_d) = (0.3, 1.1, 2.5, 0.7)$ and vary the

parameter p_e . For $p_e \geq 0$, there are five fixed points of type \mathbf{r}_1 , fixed points (S25) of type \mathbf{r}_2 , points (S26) and (S27) of type \mathbf{r}_3 , and points (S31) of type \mathbf{r}_5 . For $p_e \geq 2.1$, fixed points (S28) and (S30) of types \mathbf{r}_3 and \mathbf{r}_4 , respectively, are created. For $0 < p_e < 1.8$, all existing fixed points of types \mathbf{r}_1 , \mathbf{r}_2 , \mathbf{r}_3 , and \mathbf{r}_5 are unstable. We find a stable cycle consisting of heteroclinic orbits among saddle fixed points of types \mathbf{r}_1 and \mathbf{r}_2 . For $1.8 < p_e < 2.4$, the type \mathbf{r}_5 exists as a stable attractor, while the other fixed points are always unstable. For $2.4 \leq p_e < 8$, the global coexistence state of five species no longer exists but the fixed point (S30) becomes stable in which four species coexist. For $p_e \geq 8$, the fixed points (S30) disappear and the fixed points (S28) become stable in which three species survive. Even though the fixed points (S28) are stable, they will converge to the fixed points (S25) of type \mathbf{r}_2 for $p_e \rightarrow \infty$. It is thus possible to observe a coexistence state of two species for large values of p_e . The results of the stability analysis and numerical simulations are illustrated in the bifurcation diagram and spatial snapshots in the main text (Figs. 3 and 5, respectively).

The extinction state (S24) can be obtained from a different parameter setting such as $(p_a, p_b, p_c, p_d) = (0.01, 1.1, 2.5, 0.7)$. By varying p_e , the stable fixed point (S28) converges to the extinction state of type \mathbf{r}_1 because of the simultaneous decrease in the populations of the two species C and E , as shown in Fig. 5 in the main text.

3.2 PDE model

Similarly to the ERPS system, we obtain the PDE model for the RPSLS game as

$$\begin{aligned}
\frac{\partial a(\mathbf{x}, t)}{\partial t} &= M\Delta a(\mathbf{x}, t) + \mu a(\mathbf{x}, t)[1 - \rho(\mathbf{x}, t)] - \sigma e(\mathbf{x}, t)a(\mathbf{x}, t) \\
&\quad - \gamma a(\mathbf{x}, t)c(\mathbf{x}, t) - \frac{p_a}{2}a(\mathbf{x}, t)a(\mathbf{x}, t), \\
\frac{\partial b(\mathbf{x}, t)}{\partial t} &= M\Delta b(\mathbf{x}, t) + \mu b(\mathbf{x}, t)[1 - \rho(\mathbf{x}, t)] - \sigma a(\mathbf{x}, t)b(\mathbf{x}, t) \\
&\quad - \gamma b(\mathbf{x}, t)d(\mathbf{x}, t) - \frac{p_b}{2}b(\mathbf{x}, t)b(\mathbf{x}, t), \\
\frac{\partial c(\mathbf{x}, t)}{\partial t} &= M\Delta c(\mathbf{x}, t) + \mu c(\mathbf{x}, t)[1 - \rho(\mathbf{x}, t)] - \sigma b(\mathbf{x}, t)c(\mathbf{x}, t) \\
&\quad - \gamma c(\mathbf{x}, t)e(\mathbf{x}, t) - \frac{p_c}{2}c(\mathbf{x}, t)c(\mathbf{x}, t), \\
\frac{\partial d(\mathbf{x}, t)}{\partial t} &= M\Delta d(\mathbf{x}, t) + \mu d(\mathbf{x}, t)[1 - \rho(\mathbf{x}, t)] - \sigma c(\mathbf{x}, t)d(\mathbf{x}, t) \\
&\quad - \gamma a(\mathbf{x}, t)d(\mathbf{x}, t) - \frac{p_d}{2}d(\mathbf{x}, t)d(\mathbf{x}, t), \\
\frac{\partial e(\mathbf{x}, t)}{\partial t} &= M\Delta e(\mathbf{x}, t) + \mu e(\mathbf{x}, t)[1 - \rho(\mathbf{x}, t)] - \sigma d(\mathbf{x}, t)e(\mathbf{x}, t) \\
&\quad - \gamma b(\mathbf{x}, t)e(\mathbf{x}, t) - \frac{p_e}{2}e(\mathbf{x}, t)e(\mathbf{x}, t).
\end{aligned} \tag{S32}$$

4 Supplementary Tables

Type	\mathbf{p}_1	\mathbf{p}_2	\mathbf{p}_3
Fixed point	$(w_1, 0, 0)$ $(0, w_1, 0)$ $(0, 0, w_1)$	$w_2(p, p - 2\sigma, 0)$ $w_2(p - 2\sigma, 0, p)$ $w_2(0, p, p - 2\sigma)$	$w_3(1, 1, 1)$
λ_i	$\lambda_1 = -1$ $\lambda_2 = \frac{p-2}{2+p}$ $\lambda_3 = \frac{p}{2+p}$	$\lambda_1 = -1$ $\lambda_2 = \frac{(p-1)^2+3}{p^2+4p-4}$ $\lambda_3 = \frac{p(2-p)}{p^2+4p-4}$	$\lambda_1 = -1$ $\lambda_2 = \frac{(1-p)\pm\sqrt{3}i}{8+p}$ $\lambda_3 = \lambda_2$
Existence	always	$p > 2\sigma$ $p^2 + 4\mu p - 4\mu\sigma > 0$	always
Stability	unstable	unstable	unstable, if $p < 1$ stable, if $p > 1$

Supplementary Table S1: Existence and stabilities of all existing fixed points of RPS system (S1). For uniform intraspecific competitions, the RPS system admits three types of fixed points: $w_1 = 2\mu/(2\mu + p)$, $w_2 = 2\mu/(p^2 + 4\mu p - 4\mu\sigma)$, and $w_3 = 2\mu/(6\mu + 2\sigma + p)$.

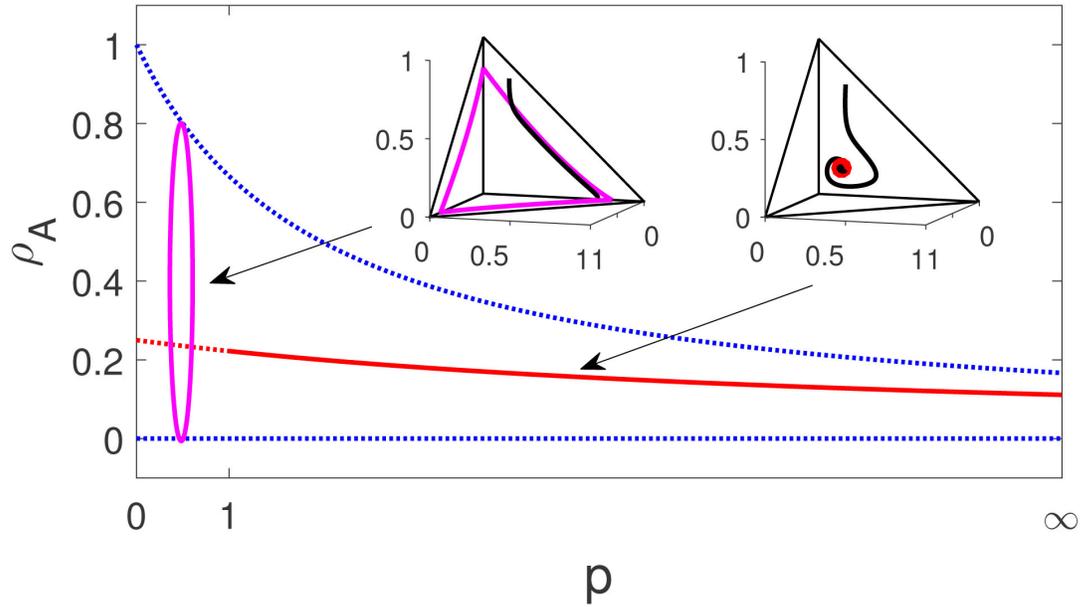
Species	AB	AC	BC
Fixed point	$w_4(p_b, p_a - 2, 0)$	$w_5(p_c - 2, 0, p_a)$	$w_6(0, p_c, p_b - 2)$
λ_i	$w_4(p_a(p_b - 2) + 4)/2$ $-w_4p_b(p_a - 2)/2$ -1	$w_5(p_c(p_a - 2) + 4)/2$ $-w_5p_a(p_c - 2)/2$ -1	$w_6(p_b(p_c - 2) + 4)/2$ $-w_6p_c(p_b - 2)/2$ -1
Existence	$p_a > 2$ $p_b > 0$ $p_b > \frac{4-2p_a}{p_a+2}$	$p_a > 0$ $p_c > 2$ $p_a > \frac{4-2p_c}{p_c+2}$	$p_b > 2$ $p_c > 0$ $p_c > \frac{4-2p_b}{p_b+2}$
Stable Condition	$p_a(p_b - 2) + 4 < 0$ $p_a > \frac{4}{2-p_b}, p_b < 2$	$p_c(p_a - 2) + 4 < 0$ $p_c > \frac{4}{2-p_a}, p_a < 2$	$p_b(p_c - 2) + 4 < 0$ $p_b > \frac{4}{2-p_c}, p_c < 2$

Supplementary Table S2: Summary of existence and stability conditions of fixed points of type \mathbf{p}_2 for RPS system (S4). For nonuniform intraspecific competitions, the RPS system allows three different fixed points of type \mathbf{p}_2 : $w_4 = 2/(p_a p_b + 2(p_a + p_b) - 4)$, $w_5 = 2/(p_a p_c + 2(p_a + p_c) - 4)$, and $w_6 = 2/(p_b p_c + 2(p_b + p_c) - 4)$ for $\sigma = 1$ and $\mu = 1$.

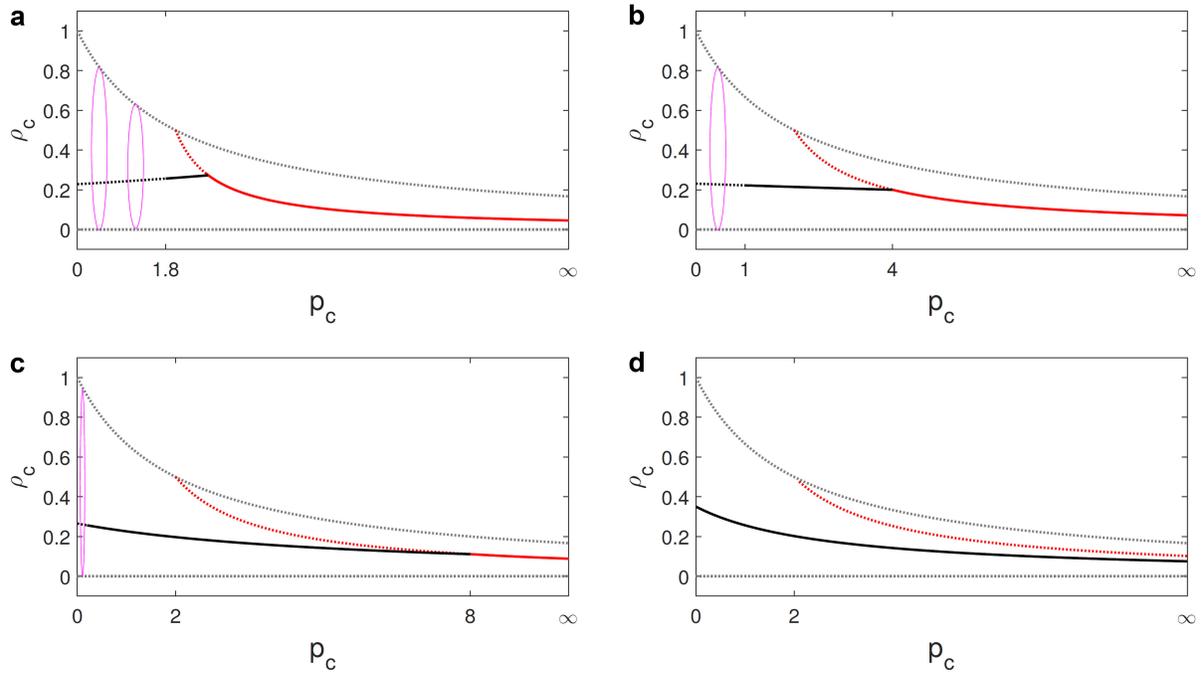
5 Supplementary References

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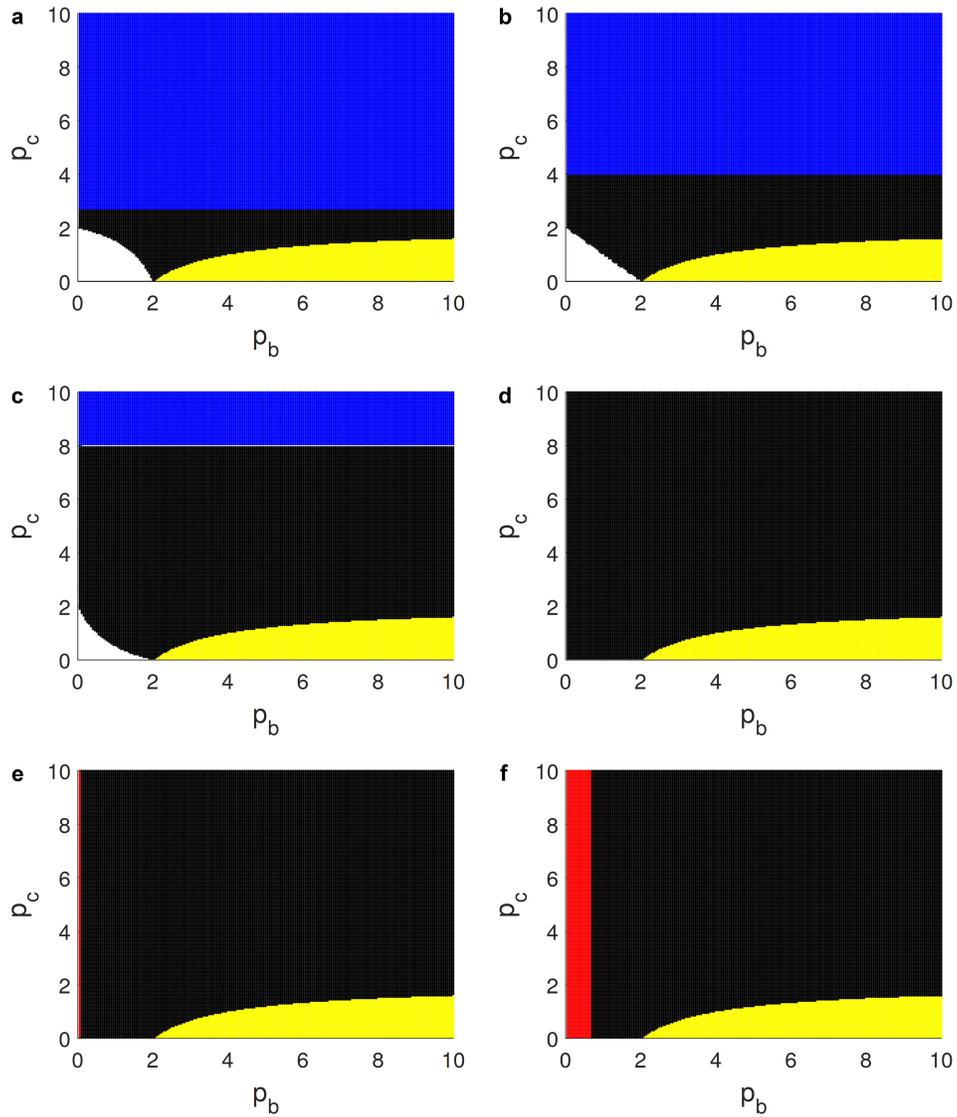
6 Supplementary Figures



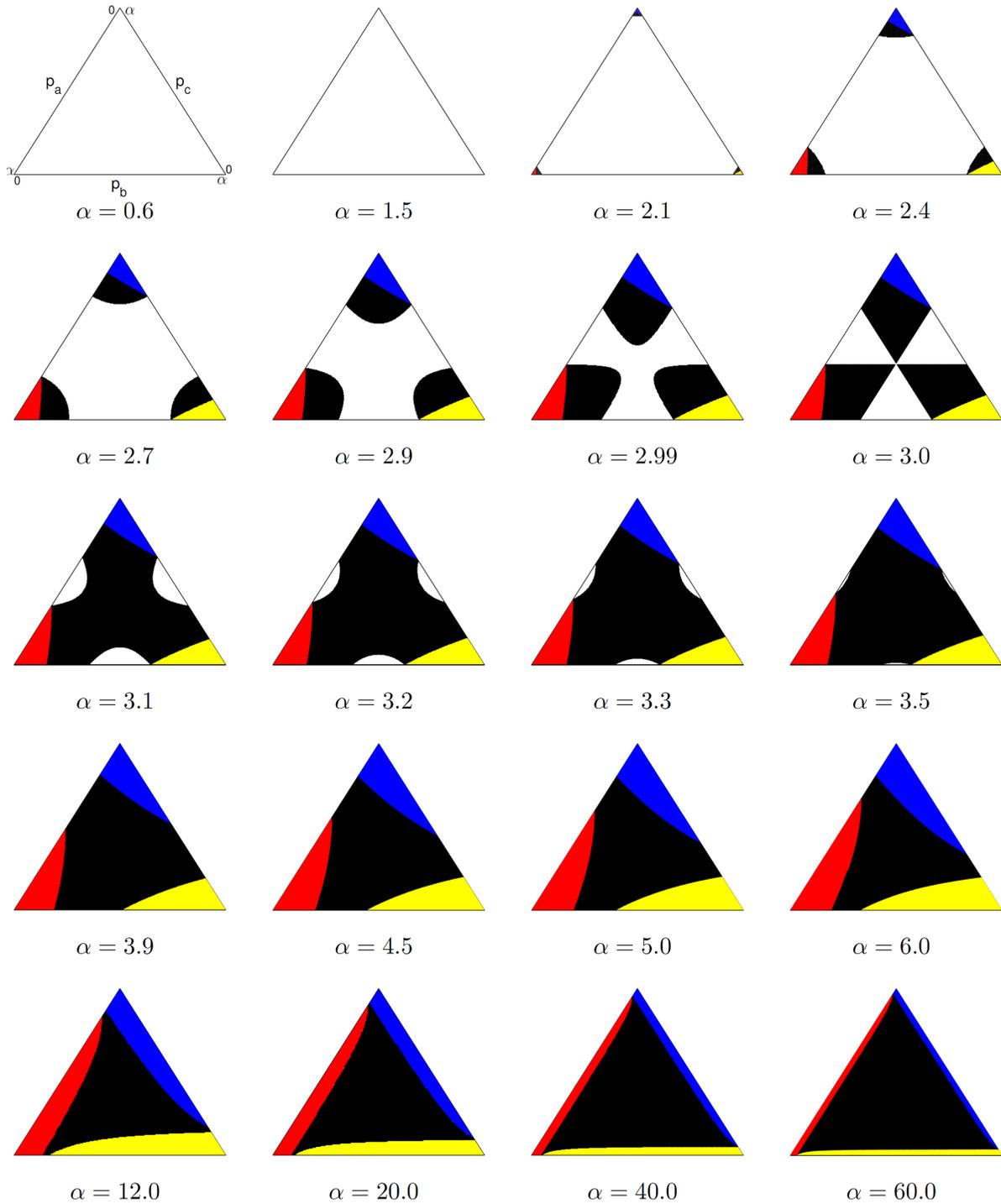
Supplementary Figure S1: Bifurcation diagram of the RPS system (S1). For $0 \leq p < 1$, an asymptotically stable heteroclinic cycle exists and the fixed point of type \mathbf{p}_3 in which all three species coexist is unstable (red dotted line). For $p > 1$, the heteroclinic cycle loses its stability and the fixed point \mathbf{p}_3 becomes stable (red straight line). Blue dotted lines represent the unstable fixed point \mathbf{p}_1 . The insets illustrate the behaviors of a typical trajectory (black), the heteroclinic cycle (connected magenta lines), and the fixed point \mathbf{p}_3 (red dot).



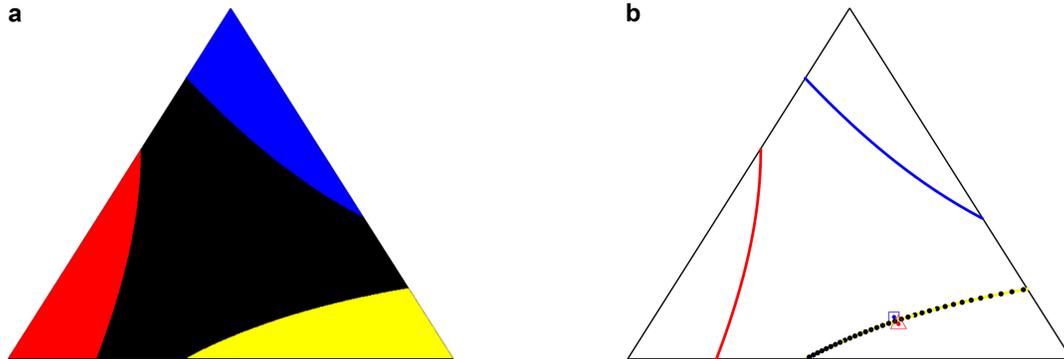
Supplementary Figure S2: Bifurcation diagrams of the RPS system (S4). For $p_a = p_b$, the values of parameter p_a from (a) to (d) are fixed at 0.5, 1.0, 1.5 and 2.1, respectively. Grey, red and black indicate three different states, \mathbf{p}_1 , \mathbf{p}_2 and \mathbf{p}_3 , respectively. Dotted and solid lines indicate unstable and stable fixed points, respectively. (a-c) As p_c is increased, after the stable heteroclinic cycles (ellipses) lose their stability, coexistence of all three species emerges, after which the coexistence state of two species is persistent. (d) For sufficiently large values of $p_a > 2$, the fixed point \mathbf{p}_3 is always stable, indicating persistent coexistence of three species.



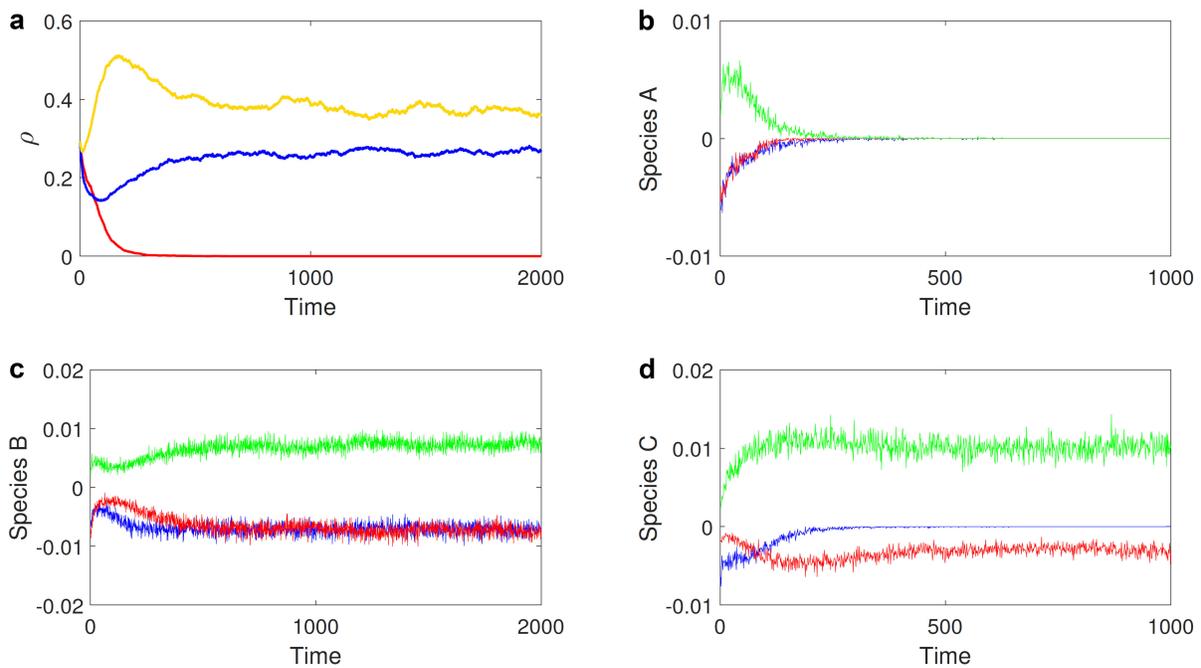
Supplementary Figure S3: Parameter regions of different attractors for fixed p_a . (a-f) For values of p_a fixed at 0.5, 1.0, 1.5, 2.0, 2.1 and 2.5, respectively, parameter regions of stable fixed points of type \mathbf{p}_3 and a stable heteroclinic cycle (black and blank regions, respectively). Red, blue and yellow areas indicate three different states of type \mathbf{p}_2 as stable attractors: AB , AC , and BC , respectively.



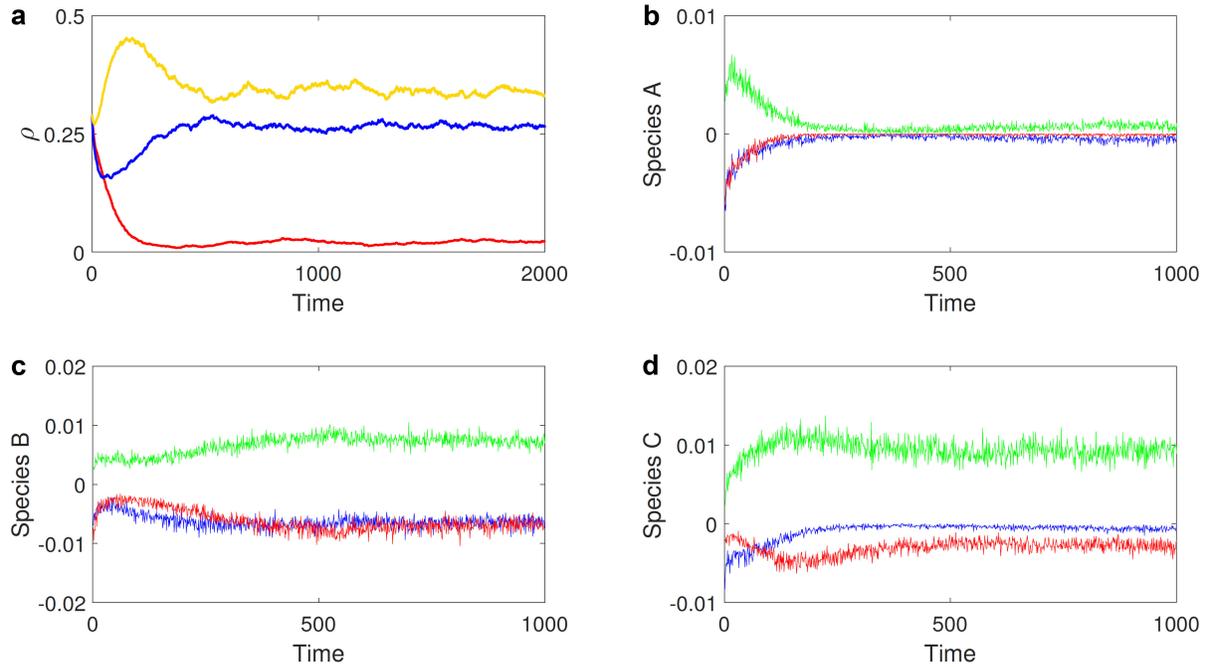
Supplementary Figure S4: Parameter basin versus total intraspecific competition rate $\alpha = p_a + p_b + p_c$ on 2-simplex. Each edge of the 2-simplex represents the parameters p_a , p_b and p_c , and its length is α . Black and blank regions indicate the parameter regions of the stable fixed point p_3 and a stable heteroclinic cycle, respectively. Red, blue and yellow areas indicate three different states of type p_2 as stable attractors: AB , AC , and BC , respectively.



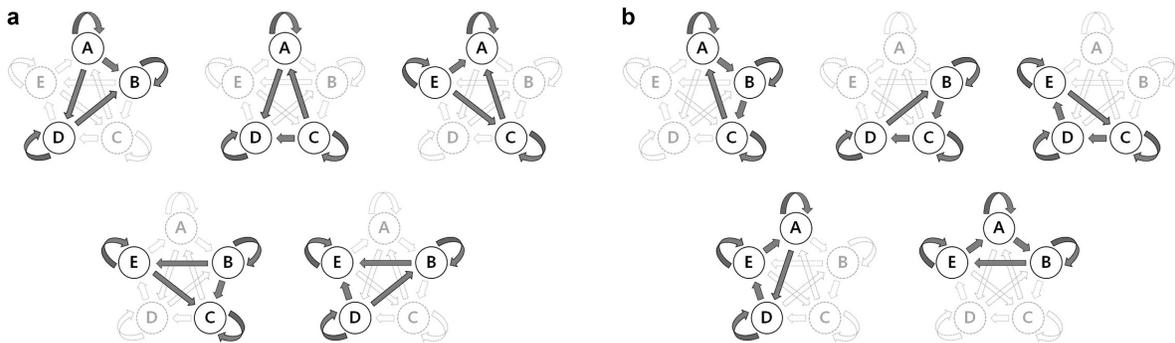
Supplementary Figure S5: Parameter basin and boundary curves for $p_a + p_b + p_c = 5$. Red, blue and yellow lines in (b) indicate the corresponding boundaries of the regions shown in (a). For instance, the yellow boundary is drawn from the equation $p_a + 4/(2 - p_c) + p_c = 5$.



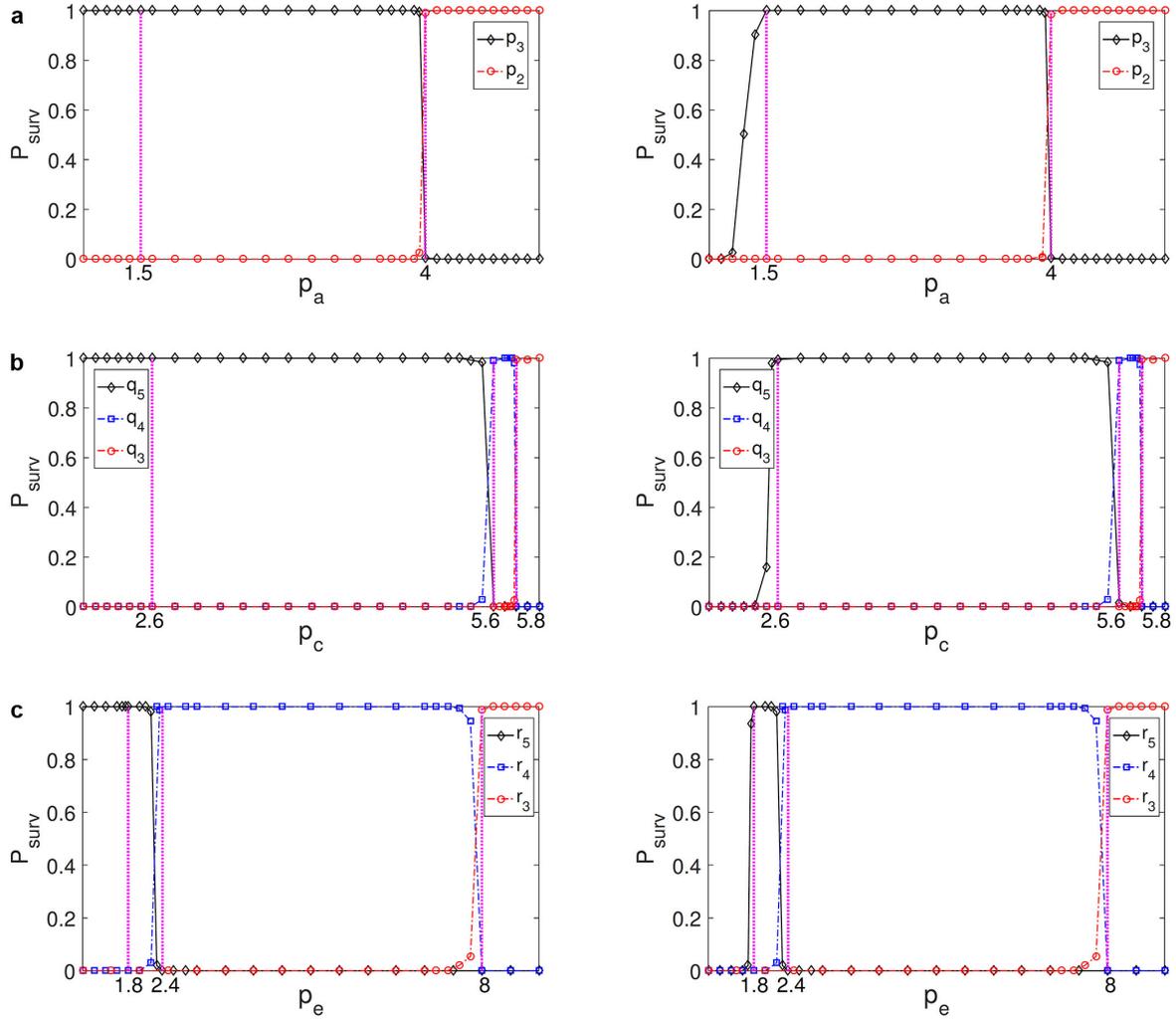
Supplementary Figure S6: Behaviors of densities from lattice simulation of RPS. For $p_a = 1.7$, $p_b = 2.8$, $p_c = 0.5$, and fixed mobility $M = 10^{-3}$, (a) densities of three species corresponding to extinction of species *A* and coexistence of species *B* and *C*. Red, blue and yellow lines indicate the densities of species *A*, *B*, and *C*, respectively. (b-d) Behaviors of species densities as a result of three types of interactions: interspecific competition (blue), intraspecific competition (red), and reproduction (green).



Supplementary Figure S7: Densities from lattice simulation of RPS system. For $p_a = 1.7$, $p_b = 2.7$, $p_c = 0.6$, and fixed mobility $M = 10^{-3}$, (a) densities of three species corresponding to extinction of species A and coexistence of species B and C . Red, blue and yellow lines indicate the densities of species A , B , and C , respectively. (b-d) Behaviors of species densities as a result of three types of interactions: interspecific competition (blue), intraspecific competition (red), and reproduction (green).



Supplementary Figure S8: Classification of fixed points of type r_3 in RPSLS system (S23). There are ten fixed points of type r_3 . (a) Five possibly stable fixed points with a non-sub-cyclic structure, (b) other fixed points having a sub-cyclic structures, which are always unstable under the existence condition.



Supplementary Figure S9: Survival probability associated with each stable phase for different cyclic game systems. (a-c) For RPS, ERPS, and RPSLS systems, respectively, the survival probabilities for two different values of the mobility: $M = 10^{-5}$ (left) and $M = 10^{-3}$ (right). In each simulation, a square lattice of 500×500 sites is used and the survival probability is evaluated from 100 independent realizations. For each system, the thresholds of robust stable phases are consistent with those from the bifurcation analysis of the underlying ODE model.