

Globally synchronized oscillations in complex cyclic games

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The rock-paper-scissors game and its generalizations with $S > 3$ species are well-studied models for cyclically interacting populations. Four is, however, the minimum number of species that, by allowing other interactions beyond the single, cyclic loop, breaks both the full intransitivity of the food graph and the one-predator, one-prey symmetry. Lütz *et al.* [*J. Theor. Biol.* **317**, 286 (2013)] have shown the existence, on a square lattice, of two distinct phases, with either four or three coexisting species. In both phases, each agent is eventually replaced by one of its predators, but these strategy oscillations remain localized as long as the interactions are short ranged. Distant regions may be either out of phase or cycling through different food-web subloops (if any). Here we show that upon replacing a minimum fraction Q of the short-range interactions by long-range ones, there is a Hopf bifurcation, and global oscillations become stable. Surprisingly, to build such long-distance, global synchronization, the four-species coexistence phase requires fewer long-range interactions than the three-species phase, while one would naively expect the opposite to be true. Moreover, deviations from highly homogeneous conditions ($\chi = 0$ or 1) increase Q_c , and the more heterogeneous is the food web, the harder the synchronization is. By further increasing Q , while the three-species phase remains stable, the four-species one has a transition to an absorbing, single-species state. The existence of a phase with global oscillations for $S > 3$, when the interaction graph has multiple subloops and several possible local cycles, leads to the conjecture that global oscillations are a general characteristic, even for large, realistic food webs.

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I. INTRODUCTION

Actual food webs are usually large and complex graphs and although their structure alone is not always enough to predict whether extinctions will occur or which species will eventually dominate, understanding the role of the specific local modules (hierarchical, tree-like, loop, dangling ends, etc.) is important when modeling competing populations. The existence of closed, oriented loops, in which the S species are not ranked, is believed to be an important mechanism fostering persistent coexistence in the presence of competition among species. In this case, each species is eventually replaced by a predator in a cyclic manner [1,2]. For $S > 3$, several partially overlapping cycles are possible, and the larger S is, the harder it is to identify the whole ensemble of interactions. Indeed, observing these trophic networks in real systems and resolving the effects of their topology and internal dynamics from noisy external causes are not simple tasks. It is thus not surprising that most of the observed examples are for small S [3,4]: mating lizards [5], competing bacteria [6–9], coral reef environments [10], competing grasses [11–13], etc. It remains necessary, though, to systematically study which properties are robust when S is large and which are specific of systems with a small number of species.

For $S = 3$, the simplest and well-studied rock-scissors-paper (RSP) game, the interaction graph is a three-vertex, single-loop-oriented graph in which all three species interact with each other. A direct generalization [14–21] considers an oriented ring with $S > 3$, $0 \rightarrow 1 \rightarrow \dots \rightarrow S-1 \rightarrow 0$ and, while nearest neighbor species along the ring interact,

the others are mutually neutral. In particular, $S = 4$ is the simplest case in which neutral pairs may form noninteracting, passive alliances that prevent or delay invasions [16–26]. On the other hand, active defensive alliances [27] may appear among non-mutually-neutral species (cyclic alliances) when the interaction graph has more than a single loop [22,28–42]. This is obtained for $S = 4$ by introducing crossed interactions with rate χ (see Fig. 1), that turn the ring into a fully connected graph and break not only its full intransitivity [42,43] but also the equal number of predators and preys symmetry. In spite of that, this model still presents a four-species coexistence phase for not too large values of χ : beyond a threshold $\chi_c \simeq 0.35$, the weakest species becomes extinct and the food web changes to an inhomogeneous RSP game.

While the system has not yet attained an absorbing state, local oscillations are observed as each agent is eventually replaced by one of its predators. That is, each site is a simple oscillator as strategies cycle in a sequence obeying the food web. In the square lattice, two of these oscillators, located at sites far apart, are not able to have these oscillations in phase. Indeed, the short-range interactions are not able to build correlations involving large portions of the system, and when the global densities are evaluated, these phase differences average out and the system attains a fixed point (up to finite-size fluctuations); that is, no oscillations in global densities are observed. In analogy to epidemiological models [44], upon the introduction of long-range interactions for $S = 3$, since the average path length between sites becomes much smaller, global synchronization becomes possible and there is a Hopf bifurcation from the fixed point to a limit cycle [32,45,46]. For more complex food webs, $S > 3$, with the simultaneous presence of several possible loops, and the possibility that distinct regions of a spatially distributed system follow different subcycles, it is not *a priori* obvious whether

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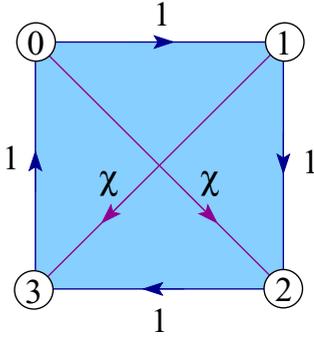


FIG. 1. (Color online) Species interactions represented by an oriented graph, arrows indicating the invasion direction and 1 and $0 \leq \chi \leq 1$ are the corresponding rates [42].

well-separated regions would be able to synchronize. This poses the question of the very existence of the Hopf bifurcation and whether global oscillations may be stable or not under the presence of several possible local cycles. Would they require a stronger correlation between distant regions and, as a consequence, a larger amount of long-range connections? Moreover, whether there is a larger or smaller species diversity when long-range interactions are introduced seems to strongly depend on the details of the updating rule chosen to model the individual interactions [36,47]. Thus, further important points are to understand to what extent the coexistence state is robust against both the change in the range of the interactions and the presence of global oscillations and how these results may be extended to other $S > 3$ systems.

To address the above questions, we study the $S = 4$ system introduced in Ref. [42] and consider a simple network that interpolates between the local square lattice, and the nonlocal random graph. In Sec. II we introduce the model and describe the topology of the food web and the spatial network. Then, in Sec. III we present our results and, finally, discuss and present our conclusions in Sec. IV.

II. MODEL, DYNAMICS, AND NETWORK TOPOLOGY

The starting model consists of a fully intransitive system of four species (or strategies), identified from 0 to 3, such that the species i outcompetes the species $(i + 1) \bmod 4$, that is, $0 \rightarrow 1 \rightarrow 2 \rightarrow 3 \rightarrow 0$ (0123, for short) with uniform, unitary rate. We break the mutual neutrality of species (0,2) and (1,3) by adding crossed interactions with a tunable rate $0 \leq \chi \leq 1$ (Fig. 1). Whenever $\chi \neq 0$, some hierarchy is present since the subloops 123 and 012 are transitive while 013 and 023 remain intransitive. Also, the symmetry of the graph is broken: while all species are equivalent if $\chi = 0$ (one prey, one predator each), for $\chi \neq 0$ they separate into two groups: species 0 and 1 have two preys and one predator, while species 2 and 3 have two predators and one prey. This strong hierarchy is attenuated by the fact that even if species 2 and 3 have only one prey each, they always subjugate them, while species 0 and 1 can sometimes fail if $\chi < 1$. Indeed, several recent works (e.g., Refs. [23,42,43,48]) have shown that the structure of the interaction graph alone is not enough to predict the asymptotic temporal evolution of the system, stressing the importance of the invasion rates.

Since we are mainly concerned with the effects of spatial correlations, the model will be studied, through Monte Carlo simulations, on a regular graph with both short- and long-range interactions and a constant number N of individuals. We start with a square lattice and periodic boundary conditions and, without changing the coordination number, replace a fraction Q of randomly chosen short-range connections with long-range ones following the rewiring process detailed in Ref. [45]. While intermediate Q produces a small world network, $Q = 0$ recovers the square lattice and $Q = 1$ a random regular graph or Bethe lattice (since typical loops, involving $\log N$ sites, become irrelevant in the thermodynamical limit). Starting from the square lattice, we choose a site and one of its nearest neighbors. The link between them is opened and reconnected to another randomly chosen, non-nearest-neighbor site (self-interactions are excluded). This last site now has an extra connection and, in order to keep the coordination constant, we remove one of its local connections. We now take the site with one neighbor missing and reconnect it with another randomly chosen site. The process is repeated until the fraction Q is reached and the graph is closed by connecting the last link freed to the missing link site of the first step. Once the rewiring finishes, no further modification in the network occurs; that is, it is quenched. There are, of course, other ways of introducing long-range interactions in the system. We chose, however, this rewiring algorithm, which replaces short- by long-range interactions, in order to (a) reproduce previous results, (b) keep the graph regular (assuming that in a time step, each agent performs a constant number of interactions), and (c) interpolate between the square lattice and the random regular graph.

The system is equally populated with all four strategies at time $t = 0$. During the time evolution, one site and one of its four neighbors are randomly chosen and their strategies are updated following the graph of Fig. 1: the predator replaces the prey with the corresponding rate, either 1 or χ . The time unit, one Monte Carlo step (MCS), corresponds to N such updating attempts. We measure the density of each strategy along the trajectory and the results below are obtained from these temporal series. This purely competitive, serial dynamics does not take into account other relevant ingredients like decoupling the reproduction and predation steps, swapping or displacement of agents, mutation, etc, although it could be extended to include them [2].

III. RESULTS

Finite systems following the dynamics described in the previous section present a sequence of extinction events, eventually attaining an absorbing, homogeneous state with a single species. These extinctions, by removing nodes and links, also change the food web, making it simpler. Nonetheless, the dependence of a conveniently defined average extinction time τ on the system size N is useful to characterize the different dynamical phases of the model [49–52]. These phases have diverse levels of diversity with either one, three, or four species coexisting [42]. For the transition from four to three coexisting species phases, the time scale of the first extinction is the relevant one [42], while for the transition to a homogeneous state is the last extinction that matters. The coexistence is said

to be stable when the related deterministic dynamics presents a stable attractor in the coexistence phase, and this is associated with an exponentially increasing time for the first extinction away from the coexistence state to occur as N increases. Analogously, the unstable state presents only a logarithmic increase of the extinction time and the deterministic system approaches an absorbing state. In between, a power-law dependence of the extinction time on the system size is related with the presence of closed, neutrally stable orbits in the deterministic case.

Let us first compare the two extreme cases, $Q = 0$ (square lattice) and $Q = 1$ (random graph). The former was studied in Ref. [42] and presents two coexisting phases without global oscillations, with either four ($\chi < \chi_c \simeq 0.35$) or three species ($\chi > \chi_c$). In these phases, the time scale of the first extinction grows, respectively, exponentially or logarithmically with N . An example of the time evolution, starting from the homogeneous state $\rho_i = 1/4 \forall i$ (black dot), is shown in Fig. 2(a). The orbit is confined to a small region around the attracting fixed point (the small volume is due to finite-size fluctuations). For the random graph ($Q = 1$), on the other hand, species 2 always becomes extinct in the early stages of the dynamics (both species 2 and 3 have two predators, but those of species 2 have two preys and are strong) and the

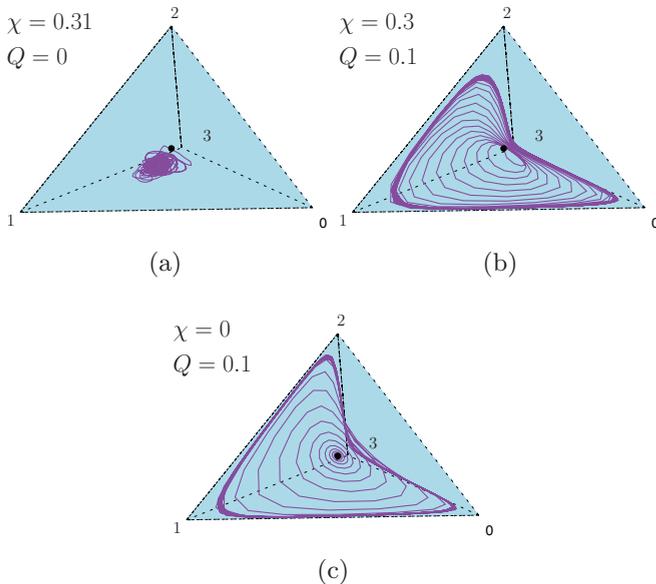


FIG. 2. (Color online) Simplex representation of the time evolution of the four densities for several values of Q and χ , showing either local or global oscillations (0123). The initial condition (black dot), is the homogeneous state $\rho_i = 1/4, \forall i$, and the system size N is large enough to prevent strong finite-size effects. (a) $Q = 0$ and $\chi = 0.3 \leq \chi_c$ for $N = 10^4$: finite size, stochastic fluctuations around the asymptotic fixed point. The amplitude of these fluctuations decreases with N [42] and all oscillations are localized. (b) $Q = 0.1$ and $\chi = 0.3 \leq \chi_c$ for $N = 4 \times 10^6$: oscillations are now global and the asymptotic state is a limit cycle whose perimeter may be used as an order parameter for the transition. (c) $Q = 0.1$ and $\chi = 0$ for $N = 4 \times 10^6$: similar to (b) but for a fully intransitive system: the orbit approaches the heteroclinic one and the average perimeter ϕ is close to the maximum value.

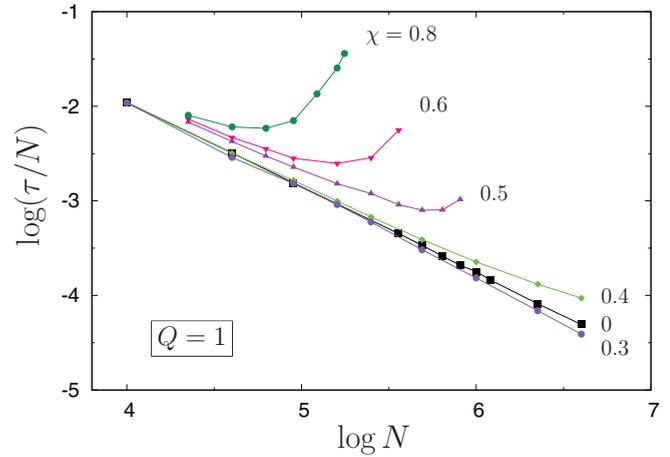


FIG. 3. (Color online) Log-log plot of the rescaled average last extinction time, τ/N vs N for $Q = 1$ (random graph). For this case, the system has two phases, with three or one surviving species and τ is the characteristic time to attain an absorbing state. Notice the presence, for large χ , of a minimum of τ/N . Before this minimum, τ depends sublinearly on N but crosses over to an exponential growth at sufficiently large sizes. For smaller values of χ , at least within the sizes and times considered here, no evidence of such a minimum is observed. At late times, there are two different regimes: if $\chi \geq 0.4$, $\tau \propto \exp N$, while for $\chi \leq 0.3$, $\tau \propto \log N$. Thus, the critical value seems to lie in the interval $0.3 < \chi_c < 0.4$.

possible asymptotic phases have one or three species for small or large χ , respectively. The relevant time scale is the time to attain the absorbing state, and it is shown in Fig. 3. Above the threshold, after an initial sublinear dependence on N (up to a crossover size, the minima in Fig. 3, for $\chi \geq 0.4$), τ enters an exponential regime. The location of the minimum grows very fast as χ approaches the threshold and seems to diverge for some value in the interval $0.3 < \chi < 0.4$. For smaller values of χ , there is no longer a minimum. This three-species phase for large χ also occurs for $Q = 0$. Thus, for large χ , it extends over the whole interval, from $Q = 0$ to 1. The level of transitivity in this case is too high to sustain four species, and the food web turns into a heterogeneous RSP game (013 with rates 1, χ , and 1, respectively). For small χ , on the other hand, the behavior is reminiscent of $\chi = 0$, in which only one- or four-species coexistence is observed since there are no cross interactions (although, in principle, two mutually neutral species are also possible). In this phase, the growth of τ is rather slow (logarithmic) and because extinctions are probable, the asymptotic state is the homogeneous, single-species phase. Interestingly, while for $Q = 0$ the system loses diversity when increasing χ , passing from four to three species, for $Q = 1$ it is the opposite, from the homogeneous single species to three coexisting ones. Diversity decreases in the former and increases in the latter.

Even more interesting is the behavior for a fixed χ as Q increases. There is a Hopf transition at Q_c from the fixed point existing at small Q to an asymptotically stable limit cycle. Two examples are shown in Figs. 2(b) and 2(c). In both cases, with both $\chi = 0$ and 0.3, the orbit approaches the four vertices in the order 0123, following the outer loop of

the food web. In the intransitive case, $\chi = 0$, Fig. 2(c), the actual path approaches the heteroclinic orbit and the system is close to the transition to the absorbing state. These global oscillations, for not so high Q , are observed in both the four- and three-species phases: while in the former the orbit is in the interior of the simplex, in the latter it is confined to one of its faces. Once in the asymptotic state, the perimeter $\phi(Q)$ of each cycle can be measured (between two consecutive crossings of the point representing the state of the system through a conveniently defined Poincaré section inside the simplex, we add up its displacement at each MC step). This is averaged over the whole evolution of the system and normalized by the perimeter of the heteroclinic orbit such that $0 \leq \phi < 1$. Figure 4 shows that the amplitude of the oscillations increases continuously with Q for different values of χ , analogous to the $S = 3$ case [45]. Above the threshold χ_c , that is, inside the three-species phase, ϕ remains smaller than its maximum value for all values of Q up to the random graph limit. In other words, the global oscillation phase extends up to $Q = 1$, consistent with Ref. [53]. On the other hand, the behavior of ϕ inside the four-species global oscillations phase, at small χ , is different as ϕ gets very close to unity, corresponding to an almost heteroclinic orbit [see Fig. 2(c)], very close to the faces of the tetrahedron. Although it is not easy to precisely locate the transition to the absorbing state as very large systems are needed in this case, our results indicate that it indeed occurs for Q not much larger than 0.3. Thus, in this case the global phase exists only for intermediate values of Q for which $0 < \phi < 1$.

A final remark concerns the exponent with which ϕ goes to 0 at the transition from local to global oscillations. In the inset of Fig. 4, for several values of χ , the declivity seems to be the same close to the transition, and the exponent is $1/2$, that is, $\phi \sim (Q - Q_c)^{1/2}$, consistent with a Hopf bifurcation. The universality of the exponent is important: it does not seem to depend neither on the original lattice structure upon which long-range connections were added nor on the complexity of the global cycle after the transition. Whether this universal

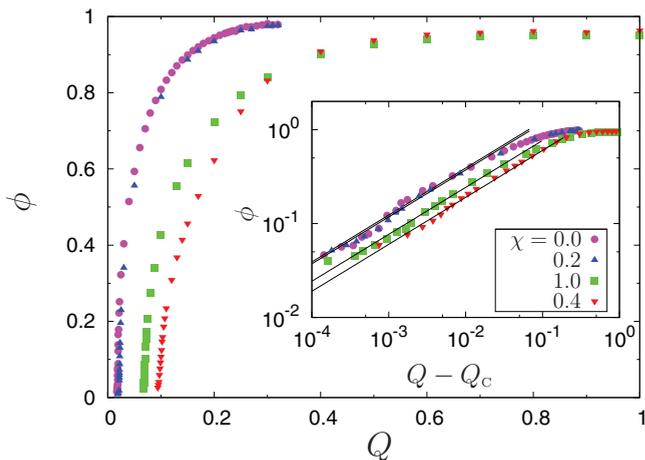


FIG. 4. (Color online) Perimeter ϕ of the limit cycle as a function of Q for several values of χ . The point at which $\phi \rightarrow 0$, $Q_c(\chi)$, locates the Hopf bifurcation from local to global oscillations. Inset: log-log plot close to the transition showing that the exponent $1/2$ does not depend on χ .

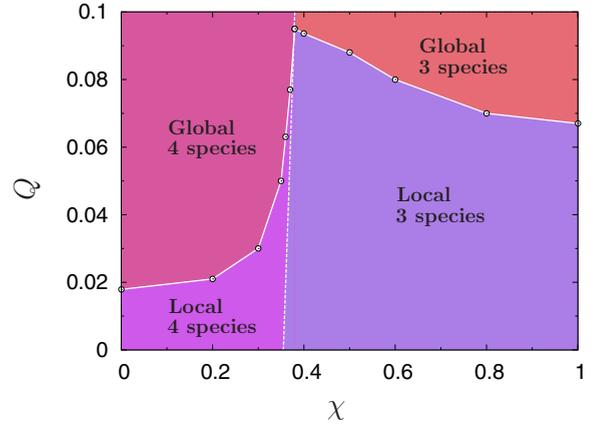


FIG. 5. (Color online) Phase diagram. The behavior at small values of Q follows the $Q = 0$ case (square lattice) studied in Ref. [42] and has a transition from a four- to three-species coexistence state. Since there is only short-range interactions, only local oscillations are present in both phases. There is a minimum amount of long-range connections, $Q_c(\chi)$, necessary to synchronize these local oscillations throughout the system. Interestingly, while the system presents coexistence of all four species (and subloops in the food web are relevant), Q_c is smaller than in the three-species phase. For even larger values of Q , the four-species phase is replaced by a less interesting single-species, homogeneous phase.

behavior is valid for even larger cycles, when $S > 4$, is an open question.

The phase diagram in Fig. 5 summarizes the above results. When the amount of long-range connections is small (low Q) only local oscillations are possible, whatever the number of species in the coexistence state. Upon increasing Q there is a transition from local to global oscillations for all values of χ . For large χ , the three-species global oscillation phase extends up to $Q = 1$. The amount of long-range interactions necessary to synchronize the oscillations, in this phase, decrease with χ : the more homogeneous the RSP food web is, the easier it is to synchronize distant regions. On the contrary, for small χ and above the local-global transition, the four-species phase has another transition, to a homogeneous single-species state (and, obviously, no oscillations). For $\chi = 0$ the amount of long-range connections necessary to present global oscillations is minimum because the food web, in this case, is a single loop. As χ increases inside this phase, one has $dQ_c/d\chi > 0$ until a maximum at the four- to three-species transition: the larger the level of transitivity of the food web is, the harder it is to synchronize. In other words, at the edge of the 4–3 transition, local oscillations are quite robust and a greater amount of long-range connections are necessary in order to correlate different regions of the system. Away from this point, either as $\chi \rightarrow 0$ or $\chi \rightarrow 1$, which corresponds to the most homogeneous conditions, the amount of long-range connections is minimum. Another interesting feature of the phase diagram is that for the three-species phase it is harder to get the global synchronization state because the necessary fraction of long-range interactions is more than three times higher than in the four-species phase. Also, for $0.067 < Q < 0.093$, the local-global transition line is reentrant as a function of χ .

IV. CONCLUSIONS

Transitivity and predation asymmetry are topological properties of oriented food webs that may prevent long-term, stable coexistence within a population. Both imply that the species are not all equivalent, but while the former is characterized by closed loops not being cyclic, the latter has species with a different number of preys and predators. Full intransitivity and symmetry ($\chi = 0$) are, however, not always required as is exemplified by the four-species coexistence in the model introduced in Ref. [42], and studied both in mean field and, through simulations, on a regular lattice. Locally, each site follows a periodic sequence of strategies allowed in the food web but these oscillations do not synchronize over long distances. Here we have shown that upon introducing a finite fraction Q of long-range interactions, well-separated regions may synchronize their local cycles and generate global density oscillations through a Hopf bifurcation even if the food web presents, in addition to multiple loops, some amount of transitivity and asymmetry. For all values of χ there is a transition from local to global oscillations occurring inside the coexistence phase. The behavior is different for small and large χ . For large χ , species 2 always becomes extinct and the remaining three-species phase, reminiscent of the $\chi = 1$ case, is stable irrespective of the value of Q . Interestingly, the amount of long-range connections necessary to synchronize the whole system decreases the larger χ is, that is, the more homogeneous the RSP cycle is. For $\chi = 0$, on the other hand, the only possible phases have either four or one species: in the absence of crossed interactions, once one species becomes extinct, the food web is no longer cyclic and only the prey of the extinct species remains. This transition, from the four-species coexistence to the absorbing state extends also for small χ and occurs when the amplitude of the limit cycle approaches the heteroclinic orbit. Interestingly enough, the number of long-range interactions necessary to obtain global synchronization, $Q_c(\chi)$, increases with χ inside the four-species phase: the more transitive are some of the subloops, the harder it is to synchronize distant regions. Again, one has the condition that

the less homogeneous is the food web, the larger is the number of long-range interactions necessary to obtain synchronization. Thus, $Q_c(\chi)$ presents a maximum close to the transition from three to four species, and it is harder to globally synchronize the density oscillations. Moreover, when all four species are present and the food web is more complex, the synchronization transition requires a smaller number of long-range interactions than for three species (and a simpler food web); that is, $Q_c(\chi)$ is smaller in the four-species phase.

At the two extremes of the phase diagram, $\chi = 0$ and 1, the system reduces to a single-loop food web with four and three species, respectively. The local to global transition occurs at $Q_c(\chi = 0) \simeq 0.018$ and $Q_c(\chi = 1) \simeq 0.068$; that is, the threshold for $S = 4$ is smaller than for $S = 3$. Whether Q_c further decreases with increasing S , approaching an effectively short-range system with global oscillations as $Q_c \rightarrow 0$, and the interplay with the fixation that may happen for large S are interesting questions that deserve further investigation.

A first step towards understanding the complex behavior of large, cyclic trophic rings is done through simplified models going beyond the standard RSP game, as the one considered here. The very existence of the local to global oscillations transition, under broad conditions, in three- and four-species models, hints of the possibility that this is a general feature even in more complex, realistic food webs. Thus, it would be important to study systems with more species ($S > 4$) in order to confirm the universality claim of the local to global oscillations phase.

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