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Cyclic competition of four species: Mean-field theory and stochastic evolution

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Abstract – Generalizing the cyclically competing three-species model (often referred to as the rock-paper-scissors game), we consider a simple system of population dynamics without spatial structures that involves four species. Unlike the previous model, the four form alliance pairs which resemble partnership in the game of Bridge. In a finite system with discrete stochastic dynamics, all but 4 of the absorbing states consist of coexistence of a partner-pair. From a master equation, we derive a set of mean-field equations of evolution. This approach predicts complex time dependence of the system and that the surviving partner-pair is the one with the larger product of their strengths (rates of consumption). Simulations typically confirm these scenarios. Beyond that, much richer behavior is revealed, including complicated extinction probabilities and non-trivial distributions of the population ratio in the surviving pair. These discoveries naturally raise a number of intriguing questions, which in turn suggests a variety of future avenues of research, especially for more realistic models of multispecies competition in nature.

editor's choice

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Introduction. – Over the years evolutionary game theory and population dynamics have yielded important insights into biodiversity and the behavior of multispecies ecological systems [1–3]. The complexity of real-world systems makes a full understanding of their properties very difficult. For that reason, the study of simple model systems is extremely valuable, as the complete knowledge of these systems allows to identify generic features valid in the more realistic but also more complex situations.

In this context multispecies models with cyclic competition constitute some of the simplest cases where coexistence and species extinction can be studied using techniques from statistical mechanics and from non-linear dynamics [3,4]. Many recent investigations revealed a rich and complex behavior. In particular, for systems with three species (also known as rock-paper-scissors game) [5–25], the results range from surprising survival/extinction probabilities in models with no spatial structure to pattern formation and mobility effects in one- and two-dimensional lattices. By contrast, far less is known for systems with more

than three species¹. Frachebourg *et al.* [5,6,26] considered M species in one dimension, $X_m + X_{m+1} \xrightarrow{k_m} 2X_m$ ($m = 1, \dots, M; X_{M+1} = X_1$), competing with equal rates, k_m . The steady states consist of single-species domains for $M = 3, 4$, but are qualitatively different for $M \geq 5$. For systems in two dimensions with slightly more complex rates, the segregation process and the formation of defensive alliances have also been studied [27–32]. In a recent paper [33] the Fokker-Planck equations for conserved quantities were derived for the $M = 3$ and $M = 4$ cases with equal competition rates. Motivated by real-world systems, some studies also focused on a large number of competing species with complicated interaction schemes [34,35].

In this paper we investigate systematically the properties of a non-spatial game involving four cyclically competing species with arbitrary rates. Not surprisingly, the behavior of the system is much richer than the three-species case [11,17]. For example, the number of absorbing states is not fixed at three (or four) but is $2(N + 1)$, where N is the number of individuals in the system. Such

¹In lattice models one sometimes speaks of four-state rock-paper-scissors games when empty sites are allowed [15,24]. In the following we do not consider empty sites to form an independent species.

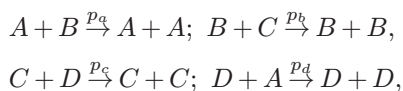
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a result can be intuitively understood, much like in the game of Bridge, where the four players form partnerships. As a result, the composition of the end state tends to be *coexistence* of partner-species, *e.g.*, L of X_1 and $N - L$ of X_3 . A mean-field approximation is formulated and studied analytically. Capturing most of the complicated time evolution of the full, stochastic model, it describes much of the rich behavior. Of course, it cannot predict extinction events. To explore those processes, we rely on computer simulations and discover very complex extinction scenarios that depend on both the rates and the initial conditions. Unlike the three-species case, our system does not support “the survival of weakest” or the “law of stay-out” [17,36,37]. Instead, the best maxim seems to be: “The prey of the prey of the weakest is the *least likely* to survive”. This result is intuitively reasonable, since the prey of the weakest survives easily and, in turn, causes *its prey* to die quickly. Notably, this maxim also applies to the three-species case, as illustrated by say, X_1 being the weakest. Then, “the prey of the prey of the weakest” is X_3 , the demise of which is excellent news for X_1 !

In the next section, we specify our model, discuss its absorbing states, and provide analytic results in a mean-field approach. Much of the system’s qualitative behavior can be understood. However, predicting extinction probabilities is much more challenging and numerical simulations for exploring them are discussed in the following section. We end with a summary and some outlook for future research.

Model specifications and mean-field theory. –

Our system consists of N individuals each of which is identified as one of four interacting species: A , B , C , and D . Endowing the species with cyclic competition, our dynamics consists of picking a random pair and letting the interactions



occur with probabilities p_m , $m = a, b, c, d$. Note that A - C and B - D pairs are *non-interacting*. Denoting the numbers of each species in our system by N_m , a configuration of the system, which has no spatial structure, is completely specified by these integers. With $N = \sum_m N_m$ being a constant, our configuration space is actually a set of points within a regular tetrahedron [38]. Unlike the cyclic competition of three species, we have $2(N + 1)$ absorbing states here. They form two fixed lines, $N_a + N_c = N$ and $N_b + N_d = N$, and describe *coexistence* of the non-interacting pairs, A - C and B - D , respectively. Moreover, note that each face of the tetrahedron is also “absorbing”, in the sense that transitions into the face are irreversible. Within each face, the problem is a special limit of the three-species model, namely, one of the three rates being zero.

From these dynamic rules, it is simple to write a master equation for $P(\{N_m\}; t)$, the probability for

finding the system t steps after an initial configuration $\{N_{m0}\}$. To find its solution is far less simple, however. Instead, we will exploit a mean-field approximation for the evolution of the averages of the *fractions*, $A(t) \equiv \sum_{\{N_m\}} (N_a/N) P(\{N_m\}; t)$, etc. Following standard routes, we start from the master equation for P and consider the large- N behavior to arrive at [39]

$$\partial_t A = [k_a B - k_d D] A; \quad \partial_t B = [k_b C - k_a A] B, \quad (1)$$

$$\partial_t C = [k_c D - k_b B] C; \quad \partial_t D = [k_d A - k_c C] D, \quad (2)$$

where $A(t)$ is simplified to A , etc. Here, t is regarded as a continuous variable and the “rates” k_m can be related to the discrete time step, the p ’s above, and N [39]. Of course, the conservation law now reads $A + B + C + D = 1$. Since an overall scale can be absorbed into t , we will follow the normalization in the literature: $k_a + k_b + k_c + k_d = 1$. The remainder of this section will be devoted to a study of the evolution of $A(t)$, $B(t)$, etc. starting with $A(0) = A_0 \equiv N_{a0}/N$, etc.

Exploiting the exponential nature of typical growth/decay, we write the above equations as

$$\partial_t \ln A = k_a B - k_d D; \quad \partial_t \ln C = k_c D - k_b B, \quad (3)$$

$$\partial_t \ln B = k_b C - k_a A; \quad \partial_t \ln D = k_d A - k_c C. \quad (4)$$

These clearly expose the alliance into opposing pairs A - C and B - D , an essential feature absent in the three-species model. Borrowing the language of Bridge, we will refer to A - C and B - D as partner-pairs, as each player works in favor of its partner and against the opposing pair. To be quantitative, we construct appropriate linear combinations such as $\partial_t [k_b \ln A + k_a \ln C] = \lambda D$, with

$$\lambda \equiv k_a k_c - k_b k_d \quad (5)$$

being a crucial parameter. In addition to controlling how each species affects the growth/decay of the opposing pair, λ generates a simple evolution

$$Q(t) = Q(0) e^{\lambda t} \quad (6)$$

for the quantity

$$Q \equiv \frac{A^{k_b + k_c} C^{k_d + k_a}}{B^{k_c + k_d} D^{k_a + k_b}}. \quad (7)$$

Similar to $R \equiv A^{k_b} B^{k_c} C^{k_a}$ in the three-species system [17], Q is t -dependent as opposed to R being *invariant*. Furthermore, since A, B, C, D are bounded by unity, the indefinite decay/growth in Q can only occur when A, C or B, D vanish. As a result, the sign of λ controls which pair survives. Intuitively, this prediction seems understandable: The pair with the larger *rate-product* ($k_a k_c$ or $k_b k_d$) wins.

Obviously, systems with $\lambda = 0$ are special, as Q is a constant of the motion. Indeed, there are *two* invariants, which can be simply $A^{k_b} C^{k_a}$ and $B^{k_d} D^{k_c}$ (as generalizations of A - C and B - D in [3,33], where $k_m = 1, \forall m$). Fixing

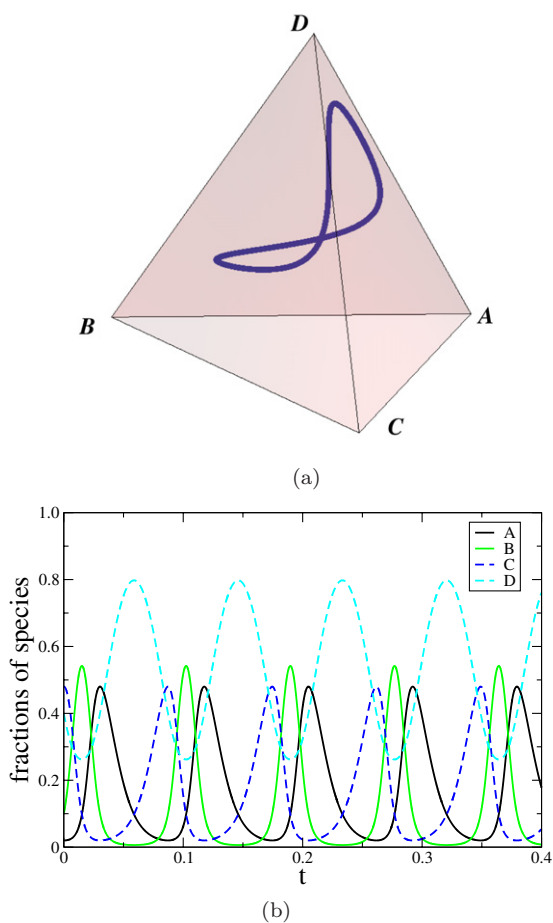


Fig. 1: (Colour on-line) An example of mean-field evolution for $\lambda = 0$: $\{k_m\} = (0.4, 0.4, 0.1, 0.1)$. (a) Closed loop in the tetrahedron forming the configuration space and (b) the fractions of the different species as a function of time. These data were generated by applying a fourth-order Runge-Kutta scheme with $\Delta t = 10^{-5}$ on eqs. (1),(2).

these by the initial conditions (A_0, B_0, C_0, D_0) , we define natural variables: $\rho_A \equiv (A/A_0)^{k_b}$, etc., which obey

$$\rho_A \rho_C = 1 = \rho_B \rho_D. \quad (8)$$

These equations define hyperbolic sheets through the tetrahedron and their intersection is a closed loop that resembles (the rim of) a saddle. Figure 1(a) shows an example of such an orbit, for the case $k_a = k_b = 0.4$ and $k_c = k_d = 0.1$. Meanwhile, fig. 1(b) shows the associated ever-lasting oscillations in A, B, C, D .

One important characteristic of a closed orbit is its extremal points. For example, let A_{\pm} denote the largest/smallest values A assumes, given an initial point (A_0, B_0, C_0, D_0) and a set of k 's. Then, A_{\pm} are solutions to a generically transcendental equation: $A_0^{-k_b/k_a} A_{\pm} + C_0 A_{\pm}^{-k_b/k_a} = \text{constant}$, which depends on B_0, D_0 , and the k 's. Typically, two distinct solutions exist, corresponding to the two extremes. At these points, the values assumed by B, C, D are, in general, not

extremal themselves. While $C = C_0(A_0/A_{\pm})^{k_b/k_a}$ at these points, B takes on the same value at both turning points: $(k_d^{k_a} k_a^{-k_a} B_0^{k_d} D_0^{k_a})^{1/(k_a+k_d)}$. Similarly, D is also unique. When $A_+ = A_-$, we are at a *fixed line* —formed by the intersection of the two planes: $k_a A = k_b C$ and $k_a B = k_d D$. Unlike the lines of absorbing states (A - C and B - D), points on this line are neither stable nor stationary under the stochastic dynamics. Being straight and bridging the A - C , B - D lines, this fixed line is enclosed by every closed orbit. In its neighborhood, these orbits approach circles, on which the system “moves” with $\omega \propto \sqrt{k_a k_c}$. Details supporting these remarks will be provided in a future publication [39].

For systems with $\lambda \neq 0$, non-trivial fixed points cannot exist (as $\ln Q \rightarrow \lambda t$). Thus, in a finite system, extinction of one of the species must occur quite rapidly. Figure 2 shows two typical cases, one for each sign of λ . Although the mean field provides good fits for short times, it predicts neither the (average) time for the first species to die out nor the composition of the other three at this extinction event. Nevertheless, we can again rely on mean-field theory *after* the system “lands” on an absorbing face (of the tetrahedron). For example, if D vanishes first and the system consists of $(A_i, B_i, C_i, 0)$ at that time, then mean-field theory predicts the system to end at a point on the A - C line: $(A_f, 0, 1 - A_f, 0)$. Here A_f is the larger of the two solutions to another transcendental equation: $A_f^{k_b} (1 - A_f)^{k_a} = A_i^{k_b} C_i^{k_a}$. As will be shown below, these predictions are born out quite well in finite, stochastic systems.

Stochastic evolution: exact and simulation results. – For a full stochastic process, there are limitations to a mean-field approach. In particular, it fails when any N_m is not “large”, *e.g.*, in small systems, or near-extinction events. If a system is “very small”, numerically exact methods can be exploited to find exact solutions to the master equation. Indeed, for the smallest, non-trivial system ($N = 4$), simple algebra is sufficient for finding analytic expressions for *all* transition probabilities (from any state to any other) and for *arbitrary* rates. Unlike $N = 3$ in three species [17] however, the results are not trivially linear (in k_m). Deferring details to elsewhere [39], we only present some general observations here. Though there is a finite probability that the “weakest” is the lone survivor, there is also a good chance for (one or both of) its *opponent pair* to survive. The clearest conclusion is: When the consumption rate of the weakest approaches zero, the survival probability of its *partner* vanishes. These considerations led us to a general maxim: “The prey of the prey of the weakest is the least likely to survive”. As pointed out above, this maxim is consistent with “survival of the weakest” in 3-species models.

For systems with larger N 's (say, $\gtrsim 100$), Monte Carlo techniques are necessary to uncover interesting behaviors in our system. To speed up the runs, we exploit the Gillespie updating scheme, in which an interaction always

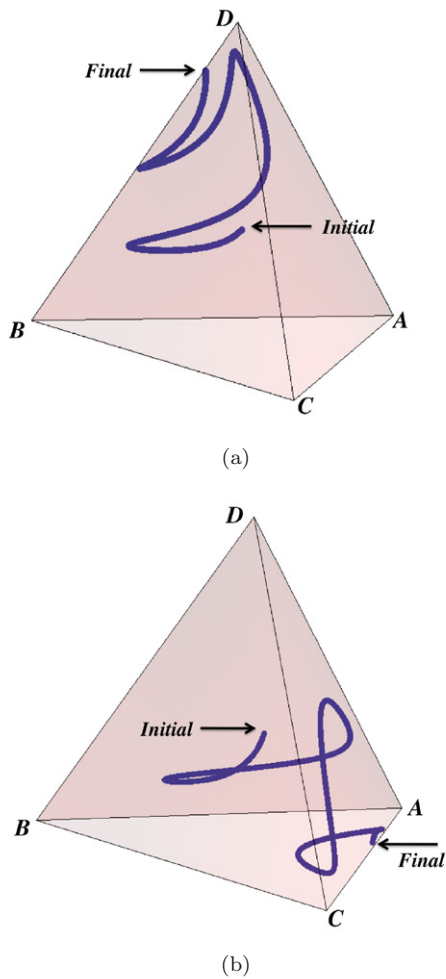


Fig. 2: (Colour on-line) Examples of mean-field evolution for $\lambda \neq 0$: (a) $\{k_m\} = (0.45, 0.33, 0.14, 0.08)$ with $\lambda = 0.0366$, and (b) $\{k_m\} = (0.35, 0.42, 0.09, 0.14)$ with $\lambda = -0.0273$. The initial fractions in both are $\{N_{m0}/N\} = (0.02, 0.10, 0.48, 0.40)$. Note the two trajectories end on the $A-C$ and $B-D$ lines, respectively. These data were generated by the same scheme as in fig. 1.

occur at each “step” (with appropriate *relative* probabilities) [40,41]. By contrast, the standard scheme is much slower, as many randomly chosen pairs do not interact. Of course, the detailed t -dependence will be quite different, so that direct comparisons with mean-field predictions are not possible. Nevertheless, we can rely on this scheme for drawing conclusions on survival and coexistence (as we can show that the extinction probabilities are scheme-independent). In particular, starting with many random initial conditions (typically 20000) and a variety of rates, simulations with $N = 100000$ confirm the mean-field predictions, namely, runs for $\lambda \neq 0$ systems ending with the correct partner pairs and runs for $\lambda = 0$ cases failing to end [42]. In the remainder of this letter, we will focus on a few particular systems with intermediate N 's, thereby emphasizing extinction processes and highlighting the differences between stochastic and mean-field trajectories.

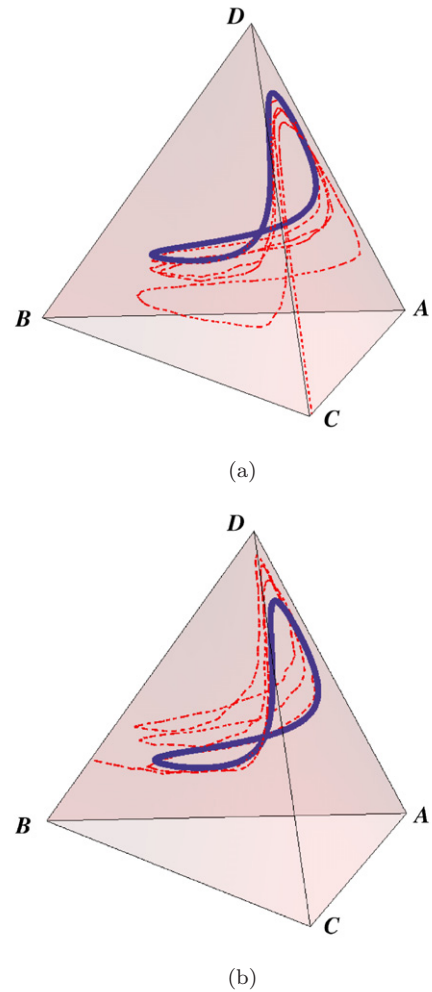


Fig. 3: (Colour on-line) Two examples of stochastic evolution (thin dashed lines, red online) of the system in fig. 1, both with $\{N_{m0}\} = (0.02, 0.10, 0.48, 0.40) \times 1000$. They follow the mean-field loop (thick line, blue online) initially, but diverge eventually, ending with opposite partner-pairs: (a) on the $A-C$ line and (b) on the $B-D$ line.

As expected, this difference is most pronounced for $\lambda = 0$ systems. Instead of closed orbits (blue online in figures), the trajectories in a finite stochastic system (red online) end in an absorbing state. In the 3-species case, they mostly end with the “weakest” species as sole survivors. In our model, no simple conclusions can be drawn. Figures 3(a),(b) illustrate a good example, where runs with identical initial conditions end very differently. Specifically, we have $N = 1000$, initial fractions $(0.02, 0.10, 0.48, 0.40)$ and rates $(0.4, 0.4, 0.1, 0.1)$. The stochastic trajectories follow these closed loops closely at early times. But, the noise drives Q away from $Q(0)$, so that they later diverge significantly and, after one of the four species dies out, end rapidly on an absorbing state. Though both runs have the *same* $\{N_{m0}, k_m\}$, the final states in figs. 3(a) and (b) consist of *opposite* partner-pairs: $A-C$ and $B-D$, respectively. In addition, there are non-trivial distributions of survival fractions within each pair (*e.g.*,

A_f , when A - C survives). Further details will be published elsewhere [39].

Systems with $\lambda \neq 0$ may appear uninteresting, as they evolve quickly towards absorbing states. However, we discover rather complex behavior, especially for systems with *extreme* rates. Let us provide one illustration, with $N = 1000$, initial fractions $(0.1, 0.7, 0.1, 0.1)$, rates $(0.1, 0.0001, 0.1, 0.7999)$ and 10000 independent trails. Since $\lambda > 0$, the survival rate of the weakest (B) is low ($\sim 10\%$), while 90% of the runs end on the A - C line. Figure 4(a) shows one particular stochastic trajectory (red online) in the latter class, as well as the mean-field orbit (blue online). Note that they come very close to the ABC face, (*i.e.*, $D \ll 1$) in two earlier occasions. Not surprisingly, in these close encounters, many runs actually “land” on this face. Figure 4(b) displays the “landing sites” (A_i, C_i with $B_i = 1 - A_i - C_i$) from these runs. Notably, they fall into three clusters (red, black, green online). Predicting the remarkable shape of the black cluster will undoubtedly be a serious challenge! From here, the system quickly evolves to the A - C line, into similarly colored clusters. Associated with the unusual black cluster shape, we find the distribution of the final A_f to be highly skewed and non-Gaussian. More details, as well as possible explanations, will be provided in a later publication. Here, let us focus on the evolution from a “landing site” (A_i, C_i) to the final point (A_f, C_f). For the ~ 9000 runs in this series, we compute $\kappa = \ln(A_f/A_i) + 1000 \ln(C_f/C_i)$ as a sensitive test of the mean-field prediction that $(A_f/A_i)^{k_b} (C_f/C_i)^{k_a} = 1$. Though not identically zero, less than 4% of the values of κ (out of the ~ 9000 values) are outside the range $[-1, 1]$! It is fair to conclude that, in this respect, the mean-field approach is extremely successful.

Summary and outlook. – In this article, we investigate the time-dependent behavior and extinction probabilities of a simple model of population dynamics: N individuals of four different “species”, competing cyclically. Though seemingly a trivial extension from a similar three-species game (rock-paper-scissors), this system displays much richer phenomena. Since the configuration space here is (the interior of) a tetrahedron rather than a triangle, trajectories of the system may twist and turn in 3d. Since the four form “partner pairs”, much like in the game of Bridge, the end states typically consists of one of the pairs, with $N - 1$ possible compositions in each case. As a result, there are $2(N + 1)$ absorbing states (instead of just 3 or 4), with generally non-trivial distributions among them. The faces of the tetrahedron are also “absorbing” (in that they correspond to the extinction of at least one species); yet the trajectories on them are not just trivial straight lines. Concerning extinction scenarios, a law gleaned from previous studies — “survival of the weakest” — seems to be violated here. Instead, our observations support, most consistently, a different maxim: “The prey of the prey of the weakest is the *least*

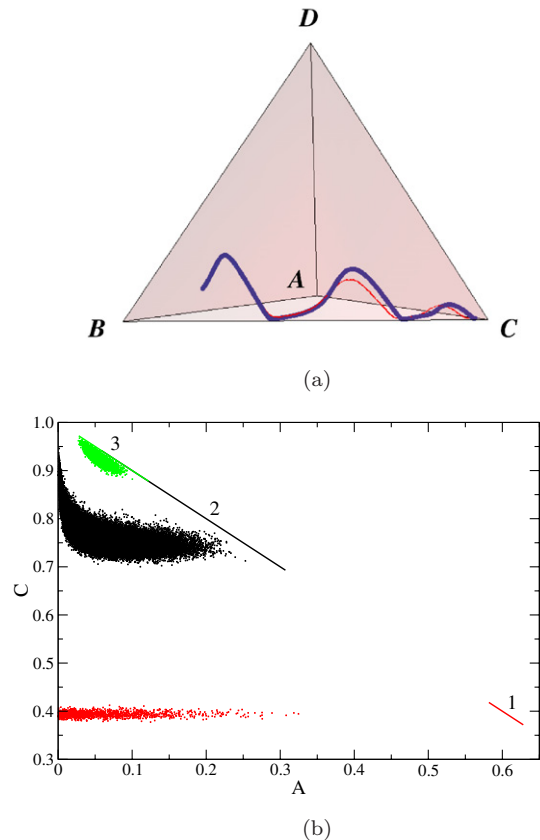


Fig. 4: (Colour on-line) A system with “extreme” rates, $\{k_m\} = (0.1, 0.0001, 0.1, 0.7999)$, starting with $\{N_{m0}\} = (0.1, 0.7, 0.1, 0.1)$. (a) One stochastic trajectory (thin dashed line, red online) and the mean-field evolution (thick line, blue online). (b) Scatter plot of the composition in 8870 runs of the system at the moment D becomes extinct (*i.e.*, “landing sites” on the ABC face), shown as three separate clusters (red, black, green online) with $A + C < 1$. Each run ends on an absorbing state (a point on the $A + C = 1$ line). Also shown is the scatter plot of these associated states, with the three clusters labeled, respectively, by 1, 2, and 3.

likely to survive”. Much easier to understand at the intuitive level, this maxim also applies to the three-species game, where the demise of the prey of one’s prey also enhances one’s survival!

Using a mean-field approach and computer simulations, we report a number of other notable findings. Similar to, but more interesting than, R in [17], our quantity Q (eq. (7)) grows/decays exponentially in mean-field theory and serves as an excellent indicator for which partner pair will survive. This theory is also quite successful in predicting the evolution of the stochastic system, as long as a) no species is close to extinction, or b) one species is extinct. These two seemingly contradictory conditions can be easily reconciled, once we are reminded that mean-field theories do not account for discrete variables (zero not being a “variable” in our dynamics!). With simulations, we discovered complex extinction scenarios (*e.g.*, non-trivial clustering in fig. 4(b)) displayed by the

stochastic model. However, to predict the properties of such distributions will be a serious challenge, as will be the task for computing the essentials of $P(\{N_m\}; t)$. Work is in progress to study a related, simpler problem: How does the distributions of R 's and Q 's evolve?

Clearly, the scope of our study is quite limited, so that many natural questions can be raised. Strictly cyclic competition in multiple species is rare in reality. What other surprises can we expect if we incorporate into our four species some of the other *twelve* possible rates? Similarly, if we introduce realistic birth/death rates (for biological species, *e.g.*), will the lack of N conservation produce novel behavior? Needless to say, the possibilities for generalization (*e.g.*, to $M > 4$ species) are limitless, even for system with no spatial structure. In fact, effects similar to those discussed here are expected for other even numbers of species [28,32]. Finally, as we noted in the introduction, qualitatively new phenomena (*e.g.*, clustering, pattern formation, moving fronts) tend to emerge when a population dynamics is placed on some underlying spatial structure. For example, in spatial systems coexistence of all four species can be maintained even for $\lambda \neq 0$ [32]. Of course, in nature, different species are likely to compete in *inhomogeneous* environments. Models that include such realistic settings [43] will certainly display a richer variety of properties and will, hopefully, lead to a better understanding of population dynamics.

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