Extinction in four species cyclic competition

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Abstract. When four species compete stochastically in a cyclic way, the formation of two teams of mutually neutral partners is observed. In this paper we study through numerical simulations the extinction processes that can take place in this system both in the well mixed case as well as on different types of lattices. The different routes to extinction are revealed by the probability distribution of the domination time, i.e. the time needed for one team to fully occupy the system. If swapping is allowed between neutral partners, then the probability distribution is dominated by very long-lived states where a few very large domains persist, each domain being occupied by a mix of individuals from species that form one of the teams. Many aspects of the possible extinction scenarios are lost when only considering averaged quantities, such as for example the mean domination time.

Keywords: coarsening processes (theory), game-theory (theory), pattern formation (theory), population dynamics (theory)
1. Introduction

In recent years, biodiversity and species extinction in ecological networks [1]–[3] have attracted an increased interest among statistical physicists [4, 5], due to the many novel, and often unexpected, features that emerge when going beyond the mean-field treatment of the simplest predator–prey models. Already, simple modifications, like adding stochastic effects [6] and/or a spatial environment [7]–[9] to the standard Lotka–Volterra model, can change species coexistence and extinction markedly. Similarly, going beyond a simple predator–prey relationship by allowing for more than two species yields interesting new scenarios that have been the focus of a range of recent studies [10]–[72].

In most situations biodiversity is only a transient phenomenon in systems characterized by species competition. Stochastic effects tend to favor species extinction in finite populations, and this even for cases where the mean-field rate equations predict ever-lasting coexistence in the form of population oscillations [34, 35, 63, 73]. The end of biodiversity can be captured by the extinction time defined as the time until the first species dies out. A closely related notion is that of fixation time in evolutionary game theory, which measures the time for one strategy to take over the entire population [74].

Extinction times have been studied extensively in situations where three species compete in a cyclic way. Of special interest are cases with symmetric rates, and we will focus on these cases in the following. When the total number of individuals is constant, the deterministic dynamics is characterized by neutrally stable, closed orbits (due to the existence of a conserved quantity [74, 28, 75]). For such a case of neutrally stable coexistence one expects that in the stochastic model the mean extinction time scales algebraically with the system size $N$. In [24, 32, 57] it was shown that for the well mixed stochastic rock–paper–scissors model the mean extinction time indeed increases linearly with $N$. For the related May–Leonard model [76], however, where the total number of individuals is a stochastic variable, the mean extinction time in the well mixed case increases logarithmically with $N$ [29]. This is readily understood by noting that in that case the deterministic dynamics yields heteroclinic orbits that are unstable.
against demographic fluctuations [5, 41]. The situation gets more complicated when considering spatially extended systems. In one space dimension it is found that for the rock–paper–scissors case the extinction time increases algebraically with the system size, but with an exponent that is larger than one. The distribution of extinction times is found to have a broad tail so that the average is dominated by rare events of long-lasting coexistence [46]. In two space dimensions the well mixed results hold for both models for large particle mobility, as this provides an effective mixing mechanism. Below a certain mobility threshold, however, the mean extinction time increases exponentially with the system size [29]. The consideration of spatially inhomogeneous reaction rates does not markedly change these scenarios [42, 46]. Extinction times have also been discussed recently for a three species cyclic model where the rock–paper–scissors and May–Leonard schemes are combined [70].

It is important to note that three species in cyclic competition form a very special case, as here every species interacts with every other species through a predator–prey relationship. When considering more than three species one has the possibility to have mutually neutral, i.e. non-interacting, species. Obviously in a real ecological environment mutually neutral species are common.

While recently an increasing number of studies have focused on cases with four or more species [10]–[13], [15, 16, 18, 20, 22, 23, 25, 27, 30, 37, 44, 45, 53, 55, 57], [63]–[69], [72], not much is known about the corresponding extinction times. In [57] the mean extinction time for the cyclic four species case is shown to scale linearly with the system size in the well mixed situation without spatial dependence. The size dependence of the mean extinction time is briefly discussed in [69] for a well mixed five species model with a more complicated interaction scheme.

In this paper we use numerical simulations to study in a systematic way extinction events in the cyclic four species case. In contrast to most of the aforementioned studies we do not solely discuss average quantities. Instead our focus is on probability distributions which are found to be non-trivial and to reflect the different stages of the competition between the species. We study the well mixed situation as well as the regular one- and two-dimensional lattices. We also present results for the four species model on the Sierpinski triangle which has a fractal dimension of approximately 1.585. Starting from a completely disordered initial state, we find that for spatial systems the probability distribution exhibits two different long time regimes. These two regimes correspond to two very different extinction scenarios.

The paper is organized in the following way. In section 2 we introduce the different versions of the four species model discussed in this paper. In section 3 we present our results for the different cases, namely the well mixed system as well as various spatially extended systems: the line, the Sierpinski triangle, and the square lattice. The focus of our study is on the probability distribution, which for the spatially extended systems is characterized by two different time scales. Section 4 gives our conclusions.

2. Model and geometries

We consider four species that undergo predator–prey interactions in a cyclic way. Calling the different species \( A, B, C, \) and \( D \), these interactions can be cast symbolically in the
form of reactions

\[ A + B \xrightarrow{\mu_a} A + A \]
\[ B + C \xrightarrow{\mu_b} B + B \]
\[ C + D \xrightarrow{\mu_c} C + C \]
\[ D + A \xrightarrow{\mu_d} D + D. \]

In this four species model we have the presence of two pairs of neutral species, namely \((A, C)\) and \((B, D)\), that do not have a predation–prey relationship. This is an important difference from the three species case where every species interacts with every other.

This reaction scheme yields the following mean-field or rate equations for the species concentrations (see [37, 45] for a detailed discussion of the mean-field results):

\[ \frac{\partial}{\partial t} a = (\mu_a b - \mu_d d)a, \quad \frac{\partial}{\partial t} b = (\mu_b c - \mu_a a)b \]
\[ \frac{\partial}{\partial t} c = (\mu_c d - \mu_b b)c, \quad \frac{\partial}{\partial t} d = (\mu_d a - \mu_c c)d \]

which can be cast in the form

\[ \frac{\partial}{\partial t} [\mu_b \ln a + \mu_a \ln c] = \lambda a, \quad \frac{\partial}{\partial t} [\mu_c \ln b + \mu_a \ln d] = \lambda b \]
\[ \frac{\partial}{\partial t} [\mu_c \ln b + \mu_a \ln d] = -\lambda a, \quad \frac{\partial}{\partial t} [\mu_d \ln b + \mu_a \ln d] = -\lambda c \]

with \( \lambda \equiv k_a k_c - k_b k_d \). Adding and subtracting these equations one discovers that the quantity

\[ Q \equiv \frac{e^{\mu_b + \mu_a \ln c + \mu_d + \mu_a}}{b^{\mu_b + \mu_a \ln d + \mu_a + \mu_b}} \]

shows a very simple dependence on time,

\[ Q(t) = Q(0)e^{\lambda t}. \]

Notice that if \( \lambda = 0 \) then \( Q(t) \) is a constant of motion for the deterministic evolution, determined by the initial concentrations. In that case the concentrations display periodic, ever-lasting oscillations.

In this work we focus on the interesting case where all predation rates are equal, i.e. \( \mu_a = \mu_b = \mu_c = \mu_d = \mu \), which yields \( \lambda = 0 \). For this case the mean-field predictions of species coexistence and population oscillations markedly differ from the domination by one of the partner pairs encountered in stochastic evolution. See [63] for an in-depth comparison between the mean-field approximation and stochastic evolution.

We consider in the following both the well mixed situation, where every agent interacts with every other, as well as lattice systems with single site occupation, where individuals located on neighboring lattice sites can prey on each other. We do not allow for empty sites, which entails that the total number of individuals in the system is conserved. We consider mobile individuals that can swap places with one of their neighbors. In the case where these two individuals have a predator–prey relationship, the swapping takes place with rate \( \sigma \), thus \( \sigma + \mu = 1 \). It can also happen that the two agents on neighboring sites are from two mutually neutral species. If that is the case, then swapping is allowed to take place with rate \( \sigma_n \) (the index \( n \) indicates that this is the rate for the swapping of neutral partners). We discuss below the two cases where \( \sigma_n = \sigma \) or 0.

Besides studying regular one- and two-dimensional lattices, with both open and periodic boundary conditions, we also simulate our four species game on a fractal. The
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Figure 1. The Sierpinski triangle after $m$ iterations. From left to right: $m = 1–4$.

The fractal we discuss in the following is the Sierpinski triangle with Hausdorff dimension $\log(3)/\log(2) \approx 1.585$. This fractal is obtained by repeatedly dividing each triangular plaquette into four solid triangular plaquettes and removing the center. Since we are interested in finite lattices, we define the depth $m$ of a Sierpinski triangle to be the number of dividing and removing iterations. Figure 1 shows the resulting lattices after the first few iterations. Every lattice point has three neighbors, with exception of the three outermost vertices which have only two. For the Sierpinski triangle of depth $m$ the total number of lattice sites is given by $3^m$. This lattice structure implies a hierarchy of bottlenecks, i.e. lattice points through which one has to go when crossing from one part of the system to another. From this point of view the Sierpinski triangle is intermediate between the chain, where every lattice site can be viewed as being such a bottleneck, and the regular square lattice, where one has many equivalent paths between different parts of the system.

If not stated otherwise we prepare the system in an initial state where every lattice site is occupied with the same probability by any one of the four species. Reactions and exchanges are then taking place between particles located on neighboring lattice sites. For every update we select a pair of neighboring sites and apply the rules given above. We increase time by one unit after $N$ proposed updates, where $N$ is the number of sites/individuals in the system. We stop the simulation when one neutral species pair, either $(A, C)$ or $(B, D)$, is occupying the whole system. The time at which this happens is then taken as our domination time. This domination time is closely related to the extinction time at which the first species goes extinct. Indeed, once a species dies out, the prey of its prey, i.e. its partner, will also be dismissed very rapidly.

In order to understand our results for the domination time, we also study the average domain size of individual species as well as the average domain size of neutral species pairs. As shown in [64], the four species on a lattice tend to arrange themselves into domains, yielding ultimately a coarsening process of domains occupied by the mutually neutral species pairs. Study of these two different domain sizes allows us to relate the different phases of the coarsening process to the different regimes displayed by the probability distribution of the domination time.

3. Domination times

3.1. The well mixed case

Let us start our discussion of the domination time $\tau$ with the simple case of a well mixed system without an underlying lattice. It has been shown in [57] that in the well mixed...
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four species case the mean extinction time increases linearly with the system size. In our simulations two particles are picked at random and allowed to perform a reaction following the scheme discussed previously. Since there is no spatial structure, we set the predation rate $\mu = 1$ (a different value of $\mu$ only rescales time). Initially, every one of the $N$ sites in the system is assigned to one of the four species with equal probability.

The probability distribution $P(\tau)$ of the domination time is shown in figure 2(a) for different system sizes. Starting from a random mix, a non-zero minimum amount of time is needed for one of the neutral species pairs to dominate. Consequently, the probability distribution rises for small times until it reaches a maximum. The decaying part is well
described by a shifted exponential distribution

\[ \tilde{P}(\tau) = \beta e^{-\beta(\tau - \tau_0)} \Theta(\tau - \tau_0) \]

(3)

where \( \Theta \) is the step function, with the shift \( \tau_0 \) and the parameter \( \beta \). This exponential distribution is a consequence of the fact that the system essentially performs an unbiased random walk in configuration space. The extinction of a species (which rapidly yields the extinction of its partner) can then be viewed as a Poisson process described by an exponential distribution. Equation (3) captures this behavior while taking into account the fact that it takes some time for a species pair to dominate when starting from a random mix.

From the probability distribution we obtain the mean domination time

\[ T = \langle \tau \rangle = \sum_{\tau=0}^{\infty} \tau \tilde{P}(\tau) \approx 0.25N \]

and the standard deviation

\[ \sigma_T = \sqrt{\langle \tau^2 \rangle - \langle \tau \rangle^2} \approx 0.14N, \]

see the inset of figure 2(a). From equation (3) the relationships

\[ \tau_0 = T - \sigma_T \quad \text{and} \quad \beta = 1/\sigma_T \]

also follow, from which one immediately deduces that the shift \( \tau_0 \) is a linear function of \( N \), whereas the parameter \( \beta \) varies inversely proportional to \( N \).

It also follows from the shifted exponential distribution (3) that data from different system sizes should collapse on a master curve when scaled properly. Indeed, exploiting directly the size dependence of the mean, \( T = T_\infty N \), and the standard deviation, \( \sigma_T = \sigma_\infty N \), as well as their relationships with \( \tau_0 \) and \( \beta \), equation (3) can be recast in the scaling form

\[ \tilde{P}'(\tau/N) = \frac{1}{\sigma_\infty} e^{\tau_\infty/\sigma_\infty} e^{-1/\sigma_\infty(\tau/N)} \Theta \left[(\tau/N) - \tau_\infty\right] \]

(4)

with \( \tau_\infty = T_\infty - \sigma_\infty \). As verified in figure 2(b), this scaling indeed works very well for the well mixed case.

3.2. Lattice systems

The four species cyclic game on the lattice is characterized by the competition between the two different teams composed of mutually neutral partners. As a result, coarsening of domains occupied by the different teams sets in \([64]\). These coarsening domains are compact and rarely contain individuals from the enemy team. In two space dimensions the domain boundaries are not very sharp, due to relentless reactions (predation and swapping) taking place at these boundaries. See \([64]\) for some configurations in one and two space dimensions. In figure 3 we show some snapshots from a typical run on the Sierpinski triangle. After preparing the system in a disordered initial state (a), small domains are rapidly formed (b), followed by a phase of domain growth (c). Due to the presence of bottlenecks that separate the lattice into different parts, one often observes that different parts of the lattice are occupied by different teams. This blocked situation can last for quite some time. For example, for the run shown in figure 3 not much is happening between the snapshots (c), taken at time \( t = 510 \), and (d), taken at \( t = 5430 \). Between these two times there are many excursions into enemy territory that fail. Eventually, one of these excursions is successful, and one of the teams takes over the whole lattice. The configuration (d) shows the beginning of that final excursion, just before the red and green species go extinct.

In order to investigate species extinction in these lattice systems, we restrict ourselves to small systems. For the line and the Sierpinski triangle the sizes range from \( N = 16 \) to
Figure 3. Snapshots of a simulation on the Sierpinski triangle with $\mu = 0.8$ and $\sigma = \sigma_n = 0.2$. The system size is 243 (iteration depth $m = 5$). The snapshots are taken at times (a) $t = 0$ (initial state), (b) $t = 9$, (c) $t = 510$, and (d) $t = 5430$ (just before the yellow–blue team dominates the system). Time is measured in Monte Carlo steps.

Figure 4 shows typical probability distributions of the domination time for the three different lattice types. While in all cases we observe an initial rise for small times and an exponential decay for long times, an additional intermediate regime is observed for the lattice systems that is absent in the well mixed case; compare with figure 2. Indeed, after the maximum a first exponential decaying regime is encountered before a crossover to the final exponential decay sets in. This final decay is much slower than for the well mixed case; see the inset. This intriguing shape of the probability distribution indicates
Figure 4. Typical probability distributions of the domination time for lattice systems. The one-dimensional chain contains $N = 81$ sites, with $\mu = 0.1$, whereas the Sierpinski triangle is formed by $N = 243$ sites, with $\mu = 0.5$. Finally, the square has $N = 45 \times 45$ sites, with $\mu = 0.6$. The swapping rates are always given by $\sigma = \sigma_n = 1 - \mu$. Inset: comparison of the well mixed (see figure 2) and Sierpinski cases with the same number of individuals, $N = 243$.

the presence of two different time scales. As discussed in the following, these two different time scales correspond to two different routes to extinction.

Possible hints at the origin of these two time scales can be found in the average domain size. Due to the presence of mutually neutral species we need to distinguish between the average size of domains that contain individuals of only one species and the average size of the larger domains formed by neutral partners. The typical time dependences of these sizes are shown in figure 5 for the line containing 243 sites. Analysis of figures 5(a) and (b) reveals three different growth regimes, in close agreement with the features in the probability distributions shown in figure 5(c).

As the initial preparation is in a random state, many small single species domains composed of only very few individuals are formed initially. Some of them will keep growing at the expense of others. In this stochastic process species are eliminated locally, which can lead in some cases to the global extinction of one of the neutral pairs, hence the increase of the domination time probability visible in figures 4 and 5(c). The local dismissal of species will be followed by an increase in the encounters of neutral species domains, resulting in the strong increase of the neutral domain size seen in figure 5(a) as well as a decrease of the domination probability function. Concomitantly the neutral species start to diffuse into each other, yielding the decrease of the individual domain size seen in figure 5(b). Once neutral domains are well mixed, it becomes very difficult for a team to take over part of the system occupied by a competing team, as every species is confronted with a mixture of predators and prey. This yields a much slower domain growth, as witnessed by the change of slope in figure 5(a), and the emergence of long-lasting transients which are revealed by the change of slope in figure 5(c). The simultaneity of these two events becomes obvious when including in figure 5(a), see the circles, the domination time where...
Figure 5. (a) Average neutral domain size, (b) average individual domain size, and (c) domination time distribution for the line composed of $N = 243$ sites. Data for different predation rates $\mu$ are shown, where the swapping rates are given by $\sigma = \sigma_n = 1 - \mu$. The dots in (a) indicate the domination times where one passes from one exponentially decaying regime to the next; see the change of slope in (c). The data result from averaging over 10,000 independent runs.
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Figure 6. Probability distributions of the domination time for the line and the square lattice with different initial conditions: random initial conditions as well as an initial state where the different teams each occupy half of the system and are arranged in such a way that every individual is surrounded by members of the partner species. The rate of the exponential decay is independent of the initial state, which indicates that these long-lived states are exclusively due to the competition of a few very large well mixed domains.

Let us add that the presence of the different regimes is a generic property of finite lattice systems, independent of the system size \( N \) and the value of the reaction rate \( \mu \), provided that a mechanism is in place that allows partner pair domains to be well mixed. Only in the limit \( \mu \ll 1 \), when particles mainly swap places, is coarsening absent, and no long-lived states are encountered in the system.

Figures 6 and 7 provide further support for our interpretation of the processes involved. We first check in figure 6 whether these long-lived states are indeed due to the presence of well mixed neutral domains. For this we prepare the system in such a way that each half of the system is occupied by one of the partner pairs. In each half the two allying species are mixed completely by having every individual surrounded by members of the partner species (with the exception of the particles located at the interface between the two halves). For the line, this yields an initial state of the form \( \cdots ACACBDBDBD \cdots \), whereas for the square lattice we have a checkerboard of \( A,C \) and \( B,D \) particles in the different halves. Figure 6 compares the probability distributions for the domination time obtained for these initial states with those that follow from random initial conditions. For both initial conditions the decay rate of the long-lived states is the same, indicating that these states are indeed due to the competition of a few very large well mixed domains.

In order to have well mixed domains composed of mutually neutral species, an efficient mechanism for the mixing of these species needs to be in place. This is realized in our system through the swapping of neutral species with the rate \( \sigma_n = 1 - \mu \). Without this swapping mechanism we would expect the long-lived states to be completely absent,

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The probability distributions of the domination time reveal many interesting features of the emerging spatio-temporal correlations due to the cyclic competition between species. It is obvious that much information is lost when only looking at the mean domination time (extinction time), as has been done in most recent studies. Still, because of the focus in the literature on this mean time, it is of interest to also discuss this quantity for our lattice systems.

Figure 8 shows the size dependence of the mean domination time $T$ for different predation rates $\mu$ and swapping rates $\sigma = \sigma_n = 1 - \mu$. The data for the square, see figure 8(a), clearly show a crossover between two regimes. For small system sizes the system behaves like a well mixed system, and the mean domination time increases approximately linearly with the system size. However, for the largest system sizes studied in this work spatial effects become important, and $T$ varies algebraically, $T \sim N^\alpha$, with an exponent $\alpha \approx 1.45$. The same crossover is also present in the one-dimensional system, see figure 8(b), but with a different exponent for the larger systems. Fitting the data for the largest three system sizes to a power law yields an effective exponent $\alpha \approx 2.10$.

Finally, we note that the same crossover is also observed in the absence of neutral partner swappings, see figure 9. However, this crossover is much more gradual, presumably due to the absence of the long-lived states where well mixed domains coarsen very slowly. Another difference between this case and that of figure 8(b) is that in the absence of neutral swappings the mean domination times increase much more slowly for larger system sizes. Indeed, for large $N$ we obtain $T \sim N^\alpha$ with $\alpha \approx 1.40$. 

whereas the earlier stages of the coarsening process, that do not rely on this swapping mechanism, should be very similar. This is indeed the case; see figure 7 where we compare for the line with $N = 81$ sites and $\mu = 0.1$ the probability distributions with and without neutral pair swappings.

The probability distributions of the domination time reveal many interesting features of the emerging spatio-temporal correlations due to the cyclic competition between species.

Figure 7. Probability distributions of the domination time for the line with and without neutral pair swappings. The long-lived states are absent without an efficient mixing mechanism between neutral partners. The system size is $N = 81$ and $\mu = 0.1$. The probability distributions result from more than 12 million independent runs.

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4. Discussion and conclusion

Stochastic evolution of a finite population of predators and prey eventually ends in species extinction and loss of biodiversity. In many instances very different routes to species extinction are possible, where the different extinction scenarios might prevail at different stages of the time evolution.

In this paper we have studied the extinction processes that are encountered in a system of four species that compete in a cyclic way. In contrast to the much studied three species models where every species is in a predation–prey relationship with every other species, the
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As a result the four species tend to form two alliances that compete against each other. We study this model both in the well mixed case without any spatial dependence and on a variety of lattices: regular one- and two-dimensional lattices as well as the fractal Sierpinski triangle. In the lattice systems our individuals are mobile and they can swap places with their neighbors. These swappings can take place between predators and prey but also between mutually neutral partners.

Our study focuses on the probability distribution of the domination time, which is the time at which one of the teams completely fills the lattice. This probability distribution is a complicated function, with various regimes which can be related to different extinction processes. In the presence of neutral pair swappings the probability distribution exhibits a crossover between two different exponential decays. The earlier regime corresponds to extinctions taking place during the coarsening of domains that contain mostly one species. The second regime, characterized by very broad tails, results from extremely long-lived states that are due to the competition of a few large domains where the members of one of the teams are well mixed. This yields a stalemate as every domain is surrounded by domains that contain a mixture of prey and predators. We have verified this scenario through simulations where we prepared the system in an initial state where each half is occupied by one team, with the team members occupying the lattice in an alternate way. In the absence of swappings of neutral partners, which provide the efficient mixing mechanism inside the domains occupied by a single team, these long-lived states are absent and the probability distribution does not exhibit this marked crossover between different regimes.

It is worth pointing out that the most prominent features of the probability distribution are independent of the lattice type. Thus, in the presence of neutral partner swappings one observes for every lattice the emergence of long-lasting states characterized

Figure 9. The same as figure 8(b), but now without swapping between neutral partners, i.e. $\sigma_n = 0$. The data result from averaging over at least 100 000 independent runs.

four species cyclic competition is a simple case where some species are mutually neutral. As a result the four species tend to form two alliances that compete against each other. We study this model both in the well mixed case without any spatial dependence and on a variety of lattices: regular one- and two-dimensional lattices as well as the fractal Sierpinski triangle. In the lattice systems our individuals are mobile and they can swap places with their neighbors. These swappings can take place between predators and prey but also between mutually neutral partners.

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by well mixed large domains responsible for the crossover between the two different regimes with exponential decay.

As the probability distributions are rather complicated, important information can be lost when looking at averaged quantities. Thus, the mean domination time $T$ as a function of the system size $N$ behaves in a qualitatively similar way with or without neutral pair swappings; even so, the corresponding probability distributions are markedly different. For a fixed value of the predation and swapping rates a crossover is observed from a well mixed situation in small systems, where $T$ increases linearly with $N$, to a lattice dominated behavior for larger systems characterized by an algebraic increase $T \sim N^\alpha$ with an exponent $\alpha > 1$. The value of the exponent is found to depend on the dimension of the lattice and on the presence or absence of neutral partner swappings.

While the details of our results are specific to the four species cyclic model studied in this paper, our study also reveals aspects that are important for other food webs characterized by competition between different species. Indeed, in a spatial environment these systems tend to yield alliances that result in more or less complicated coarsening processes [66]–[68]. In some cases a complicated dynamics takes place inside the coarsening domains. In all these cases one expects a rich variety of routes to extinction. It follows from our study that the detailed understanding of these extinction processes warrants an in-depth study of the probability distributions. Relying exclusively on averaged quantities will only allow one to gain very superficial insights into species extinction in these systems.

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