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Phase Transitions in Systems of Interacting Species

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Abstract

We discuss an autocatalytic reaction system: the cyclic competition model $A_1 + A_2 \rightarrow 2A_2$, $A_2 + A_3 \rightarrow 2A_3$, $A_3 + A_4 \rightarrow 2A_4$, $A_4 + A_1 \rightarrow 2A_1$, as well as its neutral counterpart. Migrations are introduced into the model. When stochastic phenomena are taken into account, a phase transition between a “fixation” and a “neutral” regime is observed. In the “fixation” regime, species A_1 and A_3 form an alliance against species A_2 and A_4 , and the final state is one in which one of the symbiotic pairs has won. The odd–even “coarse–grained” systems is mapped onto the two–species neutral (Kimura) model. In the “neutral” regime, all four species survive for long (evolutionary) times. The analytical results are checked against computer simulations of the model. The model is generalized for n species. Also, a generalized version of the Volterra model is analysed.

1 Introduction

There is a class of processes in which the competition plays a very important role. Examples are ecological, political, epidemiological, economic, chemical, reaction-diffusion, biological systems. An important sub-class of those is the cyclic competition systems. In ecology, cases when variants of a species compete with one-another in a cyclic fashion have been observed [1–4]. Another system of interest are cyclic food webs. In politics, different political parties compete and replace one-another in the helm of power. In the epidemiological context, examples are diseases which do not leave permanent immunity, known otherwise as *SIRS* (Susceptible-Immune-Recovered-Susceptible) models [5, 6]. Goodwin [7] introduced a system of interacting biochemical metabolic oscillators, which has an autocatalytic feedback mechanism. Biochemical reactions in a cell support its activities, hence assuring its very existence. Autocatalytic reactions are an important class of reactions within a cell. They are reputed to have made possible the birth and existence of life itself.

The simplest example of an autocatalytic reaction is the loop of the type $A_i + A_{i+1} \rightarrow 2A_{i+1}$, where $i = 1, \dots, k; A_{k+1} = A_1$. The molecules are in a well-stirred container (the cell), which is in contact with a reservoir (the outside environment). They can migrate into and out of the container, to and from the reservoir. In another (ecological) context, the $\{A_i\}$'s are versions of a biological species, and in the epidemiological one, states of an individual (e.g. susceptible, infected, etc.) In ecological systems it makes sense to also study the neutral version of this model, in which $A_i + A_{i+1} \rightarrow 2A_{i+1}$ or $2A_i$ with equal probability, corresponding to the Kimura model of neutral genetic drift [8, 9].

Duty [10] has worked on the two allele almost neutral drift model with mutations. The almost neutral model with mutations, preserving the total number of individuals, has only one degree of freedom, and allows one to derive an “effective potential” from the Fokker-Planck equation, obtained by a Kramers-Moyal expansion of the master equation. For small mutation probabilities, such that $2\mu N \ll 1$, there is extinction of one species and fixation. The effective potential is almost symmetric around the centre (where both species are in equal numbers) and the branches of the effective potential are down. This allows for the system to quickly slip into a state where only one of the species is present. Otherwise, both species coexist forever in the high mutation regime, i.e. when $2\mu N \gg 1$. In that regime, the effective potential is symmetric around the centre point, but with branches upwards, which means that the centre is a minimum potential point. The system

then remains in the vicinity of that point for very long times. The effective potential “flips” from “branches up” to “branches down” at the point where $2\mu N = 1$. The transition is second-order, and critical behaviour is observed.

In two previous studies [11, 12] we have considered an ABC model with cyclic competition/neutral drift and mutations (migrations) at a constant probability. The system exhibits a critical transition from a “fixation” regime to a “neutral” one, in which biodiversity is preserved over long time. In the “fixation” regime, the number of the A, B, C species oscillates with an amplitude that drifts with time, until one of the species (and then the second one) goes extinct, except for occasional “bursts” (which are absent when there is no migrations in the picture). In the “diversity” (or “neutral”) regime, the number of the A, B, C versions fluctuates around the centre point, and there are rare extinctions, but the product ABC remains nonzero almost always. The survival probability decays exponentially below the transition point, but the exponent decreases as the mutation (migration) probability per particle increases, until it becomes zero at the critical point. The critical mutation (migration) probability depends on system size as $1/3N$, and the models have the same power-law exponent: -1 . There is no qualitative difference between the system with mutations and that with migrations.

In the present paper we study the system with four or more species, and show that the above-described picture holds. We show that the cyclic system is a generalisation of the well-known Lotka-Volterra system, and that the size-induced transition is present in those systems as well.

2 The Model

Our system is an autocatalytic loop of the type $A_i + A_{i+1} \rightarrow 2A_{i+1}$, where $i = 1, \dots, k$; $A_{k+1} = A_1$. The molecules are in a well-stirred container (the cell), which is in contact with a reservoir (the outside environment). They can migrate into and out of the container, according to the following rules: a molecule (individual) of species i leaves the container at a rate $D \cdot a_i$, and enters it at a rate $D \cdot s_i$, where a_i and s_i are its concentrations in the cell and the reservoir, respectively. (We will assume for simplicity that the reservoir is large enough, so that the exchanges do not perturb it.) The rate equations then read:

$$\frac{da_i}{dt} = a_{i-1}a_i - a_i a_{i+1} + D(s_i - a_i) \quad (1)$$

In the rate equations approximation, the system size is conserved. The above equations (1) have a fixed point, and it is a stable solution.

The above model relates to the famous Lotka-Volterra [13, 14] model of interacting populations. A very good, and pleasant to read, review of the model has been written by Goel, Maitra, and Montroll [15]. Volterra described the system of two kinds of fish (predator-prey) by the pair of equations:

$$\begin{aligned}\frac{dN_1}{dt} &= \alpha_1 N_1 - \lambda_1 N_1 N_2 \\ \frac{dN_2}{dt} &= -\alpha_2 N_2 + \lambda_2 N_1 N_2\end{aligned}\tag{2}$$

The terms of the form $\lambda_i N_1 N_2$ describe respectively the depletion of the stock of fish 1 and the enrichment of that of fish 2 from eating fish 1, and those of the form $\alpha_i N_i$ the evolution of the species i in absence of the other. Further on, he generalized the pair of equations (2) to n species:

$$\frac{dN_i}{dt} = k_i N_i + \beta_i^{-1} \sum_{j=1}^n a_{ij} N_i N_j\tag{3}$$

In absence of other species, the i -th species will grow or die exponentially, depending on the sign of k_i . The constants a_{ij} will be positive, if species i eats j , negative, if it is eaten by j , and zero, if they do not interact at all. This leads to $a_{ij} = -a_{ji}$.

The mean-field (rate equations) behaviour of the system is well-known. It accepts periodic solutions, as shown by Volterra. Statistical mechanics of the Volterra system was first constructed by Kerner [16]. Goel et al. [15] studied the existence and stability of the solutions to the rate equations. They also introduced a random function of time (noise) in the growth equation, obtaining a Liouville equation. The model is indeed one of the simplest of nonlinear competition models.

Jain and Krishna [17] use directed graphs to describe autocatalytic sets. Directed graphs are a set of ‘nodes’ and ‘links’, where each link is an ordered pair of nodes [18, 19]. A graph with p nodes is specified by its adjacency matrix C , defined in such a way that the $c_{i,j}$ element is one, if the graph contains a link directed from node j to node i and zero otherwise. For any non-negative matrix, the Perron-Frobenius theorem [20, 21] states that there exists an eigenvalue which is real and larger than or equal to all the other eigenvalues in magnitude. It has been shown [22] that when a graph

has a closed loop, the Perron-Frobenius eigenvalue of its adjacency matrix is exactly 1. The set of Perron-Frobenius eigenvectors is of interest to us, since it provides the attractors for the dynamical system whose evolution is described by the set of differential equations:

$$\dot{a}_i = \sum_{j=1}^s c_{i,j} a_j - \phi a_i \quad (4)$$

which is equivalent to the generalized Volterra equation:

$$\dot{a}_i = \sum_{j=1}^s c_{i,j} a_j - a_i \sum_{k,j} c_{kj} a_j \quad (5)$$

when the catalysed reaction is much faster than the one described by the first term (the spontaneous one). The system will then converge towards the fixed point that is a Perron-Frobenius eigenvector of the graph's adjacency matrix. In the case of our cyclic systems, the Perron-Frobenius eigenvalue is one, and the components of the corresponding eigenvector are all equal. This means that, in the rate equations approximation, the symmetric system (with all the rates equal to one) will approach the centre (all a_i 's are equal), and remain there.

A description of the newest techniques of stability analysis for such systems can be found in [23], and the references therein.

However, the rate equations are just a “mean field” approximation; they only describe the behaviour of the average values of the individual populations. In the real world, the system is subject to stochastic noise due to birth and death processes (intrinsic noise), which we take to be Poisson-distributed. The random nature of these processes need be taken into consideration, if we want to obtain the correct and complete behaviour of the system. For that we ought to write the master equation, and then somehow solve it. Unfortunately, very few master equations are simple enough to accept analytical solutions. We deal with this situation by expanding them into a Fokker-Planck equation, which then helps us draw the necessary information about the behaviour of the system. Another approach is to simulate the master equation of the system.

The master equation for, say, the four-species cyclic system is:

$$\begin{aligned} \frac{\partial P(A_1, A_2, A_3, A_4, t)}{\partial t} = & \frac{1}{N} \left[(\epsilon_4 \epsilon_1^{-1} - 1) A_1 A_4 + (\epsilon_1 \epsilon_2^{-1} - 1) A_1 A_2 + \right. \\ & \left. + (\epsilon_2 \epsilon_3^{-1} - 1) A_2 A_3 + (\epsilon_3 \epsilon_4^{-1} - 1) A_3 A_4 \right] P(A_1, A_2, A_3, A_4, t) \end{aligned} \quad (6)$$

where we have used the “shift” operators notation:

$$\begin{aligned}\epsilon_1 f(A_1, A_2, A_3, A_4) &= f(A_1 + 1, A_2, A_3, A_4) \\ \epsilon_1^{-1} f(A_1, A_2, A_3, A_4) &= f(A_1 - 1, A_2, A_3, A_4)\end{aligned}\tag{7}$$

and similarly for the other concentrations.

3 System-Size Expansion of the Master Equation

For systems like the one above, where the rate equations have a stable solution, the Ω -expansion of van Kampen [24] works exceptionally well. Previously we have used it to solve a three-species cyclic and neutral system in presence of mutations and migrations [12].

Using the “shift” operators notation (7), the master equation for the cyclic competition system with migrations reads:

$$\begin{aligned}\frac{\partial P(\{A_i\}, t)}{\partial t} &= \left\{ \frac{1}{N} \left[(\epsilon_1 \epsilon_1^{-1} - 1) A_1 A_4 + (\epsilon_1 \epsilon_2^{-1} - 1) A_1 A_2 + \right. \right. \\ &+ (\epsilon_2 \epsilon_3^{-1} - 1) A_2 A_3 + (\epsilon_3 \epsilon_4^{-1} - 1) A_3 A_4 \Big] + D [(\epsilon_1 - 1) A_1 + (\epsilon_2 - 1) A_2 + \\ &+ (\epsilon_3 - 1) A_3 + (\epsilon_4 - 1) A_4 + \frac{N}{4} (\epsilon_1^{-1} + \epsilon_2^{-1} + \epsilon_3^{-1} + \epsilon_4^{-1} - 4)] \Big\} P(\{A_i\}, t)\end{aligned}\tag{8}$$

The idea of the van Kampen expansion [24] is to split the variables of the problem into a non-fluctuating part, and a fluctuating one, i.e. deal separately with the mean-field solutions and the fluctuations (which are taken to be of the order \sqrt{N}). In this approach, the numbers of the individual populations would be written as:

$$A_i = N\phi_i + \sqrt{N}x_i\tag{9}$$

Here the ϕ_i are the steady-state (non-fluctuating) concentrations of the i -th species respectively (which only depend on time), and the x_i are the fluctuations (proportional to the square root of system size). Then the probability distribution $P(A_i, t)$ is transformed into $\Pi(\{x_i\}, t)$, and the following relations are true:

$$\begin{aligned}\Pi &= N^2 P(N\{\phi_i + \sqrt{N}x_i\}, t) \\ \frac{\partial P}{\partial t} &= \frac{1}{N^2} \frac{\partial \Pi}{\partial t} - \frac{1}{N} \sum \frac{d\phi_i}{dt} \frac{\partial \Pi}{\partial x_i}\end{aligned}\tag{10}$$

and

$$\begin{aligned}\epsilon_i &= 1 + \frac{1}{\sqrt{N}} \frac{\partial}{\partial x_i} + \frac{1}{2N} \frac{\partial^2}{\partial x_i^2} + \dots \\ \epsilon_i^{-1} &= 1 - \frac{1}{\sqrt{N}} \frac{\partial}{\partial x_i} + \frac{1}{2N} \frac{\partial^2}{\partial x_i^2} + \dots\end{aligned}\tag{11}$$

Next we substitute everything into the master equation, leave only the term $\partial\Pi/\partial t$ on the left hand side, and group the right hand side terms according to powers of \sqrt{N} . The first term is of order $N^{1/2}$, and it must be equal to zero, for an expansion in terms of $N^{1/2}$ to make sense. That term reproduces the rate equations in terms of the concentrations ϕ_i , with steady state solution $\phi_i = 1/4$.

The terms of order N^0 give a linear Fokker-Planck equation of the form:

$$\frac{\partial\Pi}{\partial t} = \sum [-A_{ik} \frac{\partial}{\partial x_i} (x_k \Pi) + \frac{1}{2} B_{ik} \frac{\partial^2 \Pi}{\partial x_i \partial x_k}] \tag{12}$$

where the A-matrix for the cyclic system is:

$$\begin{pmatrix} \phi_4 - \phi_2 - D & -\phi_1 & 0 & \phi_1 \\ \phi_2 & \phi_1 - \phi_3 - D & -\phi_2 & 0 \\ 0 & -\phi_3 & \phi_2 - \phi_4 - D & -\phi_3 \\ -\phi_4 & 0 & \phi_4 & \phi_3 - \phi_1 - D \end{pmatrix}$$

and for the neutral system:

$$\begin{pmatrix} -D & 0 & 0 & 0 \\ 0 & -D & 0 & 0 \\ 0 & 0 & -D & 0 \\ 0 & 0 & 0 & -D \end{pmatrix}$$

The B-matrix is the same for both systems. Its diagonal elements are $B_{ii} = D(s_i + \phi_i) + \phi_i(\phi_{i-1} + \phi_{i+1})$, and the off-diagonal ones: $B_{ij} = -\phi_i\phi_j$. The Fokker-Planck equation obtained this way is linear, and the coefficients depend on time through ϕ_i . We are interested in fluctuations around the steady state. This approximation is otherwise known as “linear noise approximation”. The solution is known to be a Gaussian; the problem represents itself as an Ornstein-Uhlenbeck process. For our purposes, it suffices to determine the first and second moments of the fluctuations. Following van Kampen [24], we can multiply the Fokker-Planck equation by x_i and integrate by parts to get:

$$\frac{d\langle x_i \rangle}{dt} = \sum_j A_{ij} \langle x_j \rangle \quad (13)$$

For simplicity we can assume that all the concentrations in the reservoir are equal: $s_i = s = 1/4$. The eigenvalues of the A matrix are $-D$ (doubly-degenerate), $-D \pm i\phi\sqrt{2}$ for the cyclic system, and $-D$ (quadruply degenerate) for the neutral system. Here ϕ is the steady state value of the concentrations (we have dropped the index, since they are all the same). The negativity of the eigenvalues guarantees the stability of the zero solutions to the first moments equations. Hence, the average of the fluctuations decays to zero and remains zero. The equations for the second moments can be obtained similarly:

$$\frac{d\langle x_i x_j \rangle}{dt} = \sum_k A_{ik} \langle x_k x_j \rangle + \sum_k A_{jk} \langle x_i x_k \rangle + B_{ij} \quad (14)$$

They depend on time through ϕ_i 's, which we again substitute by their steady state value, since we are interested in the fluctuations around that state. Also, by symmetry, all the diagonal terms $\langle x_i^2 \rangle$ are equal, as well as off-diagonal terms (correlations) $\langle x_i x_j \rangle$. They depend on the migration probability D alone. The steady state solutions for the diagonal terms (and also for the variances, since the mean values are zero), are as follows:

$$\langle x_i^2 \rangle = \frac{(2\phi^2 + D(\phi + s))}{2D} \quad (15)$$

where s is the concentration of any of the species in the reservoir. The number of individual species will fluctuate around $N \cdot \phi_s$ where ϕ_s is the steady-state concentration. All the species survive forever. This way, (sufficient) migrations into and out of the container maintain diversity in the system.

It is important to point out that from the expression for the A -matrix above, we can tell that when migrations are absent ($D = 0$), the (real part of all) eigenvalues of that matrix become zero, and the equation is of the diffusion type [24]. In that case, the rate equations suggest that the non-fluctuating part will remain constant (at the centre). However, small deviations give rise to large differences, and one would expect the fluctuations to grow, rather than remain limited. The separation into a macroscopic part and small fluctuations is no longer meaningful. In this case, after a transient period (of the order $N^{1/2}$), one would expect P to be a smooth function of the concentrations, and expand in powers of N ,

rather than $N^{1/2}$. This is otherwise known as Kramers-Moyal expansion, and we have employed it for the three-species systems [11, 12], in very good agreement with the simulations results.

Furthermore, the only difference between the three and four species systems expansion is the appearance of an “off-diagonal” of zeroes, in positions (i, j) for which the species A_i and A_j do not react. This means that the above algebra will remain exactly valid when there are more than four species in the system. Hence, our results will hold for any number of species, and any reasonable system size.

If there is only migrations into and out of the container (i.e. no cyclic reactions), the system remains near the centre point, and the product of the concentrations remains considerably above zero; in other words, all species are present in the system at (almost) all times. When both the cyclic/neutral mechanism and migrations are present, one can occasionally observe temporary extinctions. Since the boundary is not absorbing, occasional migrations will return the system to the state with maximal symmetry (diversity) where all species coexist. The migrations then manage to keep the system maximally disordered, since they are stronger than the fluctuations (which try to drive the system toward the boundary, i.e. fixation, and keep it there). The migration rate acts then as some sort of “temperature”, and decreasing the migration rate would be analogous to annealing the system.

4 The Transition Region

In two papers, Togashi and Kaneko [25, 26] focus on the four-species autocatalytic system with a very small number of molecules. Their work covers many aspects of a transition, which they baptize “discreteness-induced”. The idea of their work is that, when the number of molecules in the system is very small, a transition from the state where the numbers of molecules of the individual types are Gaussian-distributed, as derived above, to one in which the A_1 and A_3 species form an alliance against species A_2 and A_4 is observed. In their work they keep the diffusion rate D constant, and vary the system size. As the total number of molecules (system size) decreases and goes through a certain value (which coincides with $1/D$, the inverse of migration rate), they observe a transition into the broken-symmetry state. One of the symbiotic pairs eventually wins, but, since there are migrations into and out of the container happening all the time, the introduction of a member of the opposite symbiotic pair may bring the victory of that initially (almost) non-existent pair, making the pair that previously was the “winner

of the hour” disappear, and so on. The probability distribution of the number $z = (x_1 + x_3) - (x_2 + x_4)$ (corresponding to our $(a_1 + a_3) - (a_2 + a_4)$) is shown in Fig. 2 of their article [25], and the formation of the peaks that indicate the (temporary) victory of one such symbiotic pair over the other as the system size goes through $1/D$ is quite pronounced. In Fig. 4 of their PRL article [25] Togashi and Kaneko show a plot of the rate of residence of the 1-3 (or 2-4) rich state (i.e. the state in which one of the pairs “rules”) as a function of the product DV (V is system size, the parameter we call N). The rate of residence of the symmetry-broken state clearly goes to zero, as $DV \rightarrow 1$.

Looking at the expression for the variance of the fluctuations above (15), one can observe that when the migration probabilities per particle (migration rate) approach zero, the variance of the concentrations of individual populations is of the order $\frac{(2\phi^2 + D(\phi+s))}{2D}$, and it becomes of order 1 (i.e. the order of macroscopic concentrations,) when $D \sim 1/N$ (here we are using the values of parameters as chosen by Togashi and Kaneko [25], who assume all $\phi_i = s_i = 1$. However, it works exactly the same way with our steady state values $\phi_i = s_i = 1/4$). This gives us the critical value for the migration probability. The critical D thus obtained is in excellent agreement with the one Togashi and Kaneko observe and show in Fig. 2 of their letter [25], when they see the system go through a transition for $V(N) = 1/D$. Also, this verifies the other result of their simulations, shown in Fig. 4 of their letter [25], where the rate of residence of the symmetry-broken state approaches zero, as $DV \rightarrow 1$. In our work on three-species systems [11,12] we have obtained similar results using van Kampen expansion, and verified them in the diffusive (fixation) regime, using a Kramers-Moyal expansion, having imposed the condition that the system be near a critical transition, i.e. the smallest eigenvalue of the Fokker-Planck equation be zero. The agreement between the two is excellent.

5 Steady-State Solutions of the Rate Equations and Simulations Results in the Fixation Regime

It is important to know the behaviour of the system, when it is closed, i.e. no migrations into and out of the container are possible, since the final state in the fixation (broken-symmetry) regime is the same. The rate equations for this system, written for the concentrations of individual species, will be:

$$\frac{da_i}{dt} = a_{i-1}a_i - a_i a_{i+1} \quad (16)$$

and similarly for the other species. If we consider the case when $A_i + A_{i+1} \rightarrow 2A_i$ or $2A_{i+1}$ with equal probability, the right-hand side of the rate equations will be identically zero.

One can directly find the steady-state solutions of the rate equations (16), i.e. the concentrations that reduce the left-hand side to zero. For any number of species in the system, the centre, where all the concentrations are equal, is a solution of the rate equations (16). When three species are present, the other solutions are those for which one of the species is alive, and the others are extinct. In the case of four and five species, the solutions are of the form $a_i = a_{i+2}$ (modulo 4 or 5, depending on the number of species in the system) with all the other concentrations equal to zero. The system with six species, except for the centre, has two other kinds of sets of solutions: one with $a_i = a_{i+2} = a_{i+4}$ (modulo 6) and all the others zero (i.e. three species alive and three dead), and one set with $a_i = a_{i+3}$ (modulo 6) with the rest of concentrations equal to zero (i.e. two “opposite” species alive and four dead). For any numbers of species in the system, the product of concentrations is conserved, as well as the total number of individuals. This means that any trajectory with the product of concentrations constant will be a neutrally stable one. In the case of the neutral systems, the right-hand side is identically zero, which means that any state is a stable one.

We simulated copies of the four- or more-species cyclic system, for different system sizes. These simulations started with equal individual populations of A_1 , A_2 , A_3 , and A_4 (i.e. the centre). We generated times for the next possible reaction event with exponential distribution as $-\frac{\ln(rn)}{\text{rate}}$, where the rate of the cyclic or migrations as in the master equation above (6) is substituted. (Here rn is a random variable with uniform distribution in $[0, 1]$. This way we get Poisson distribution for the events, i.e. really independent events [27].) The reaction which occurs first is then picked and the system is updated accordingly. The process is repeated for a large number of events. We observed the symmetry-breaking phenomenon for any system size, no matter how large it is.

In Fig. 1 we show the time series for the four-species cyclic system, for $N = 40\,000$. Contrary to the prediction from the solutions to the rate equations, for the six-species systems, out of two thousand realisations of the system, we never obtained a final state with only two species present. All the copies of the system we simulated ended up with three species present, as the time series shown in Fig. 2. In all the time series, time is measured

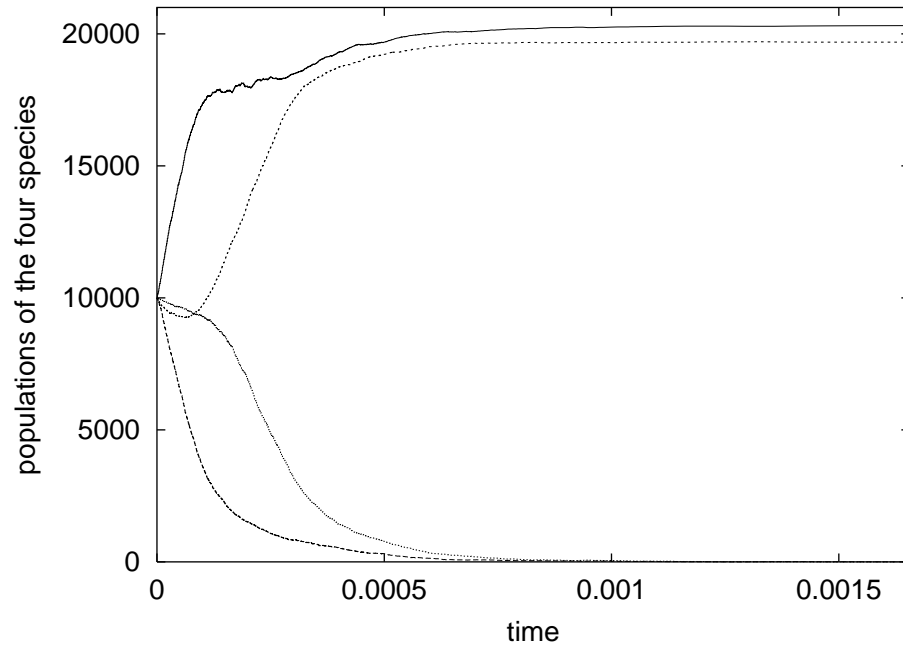


Figure 1: The time series for the number of A_1 , A_2 , A_3 , and A_4 species in the “fixation” regime (here $D = 0$, and system size $N = 40\,000$). In this particular realization the A_1A_3 symbiotic pair wins over the A_2A_4 one.

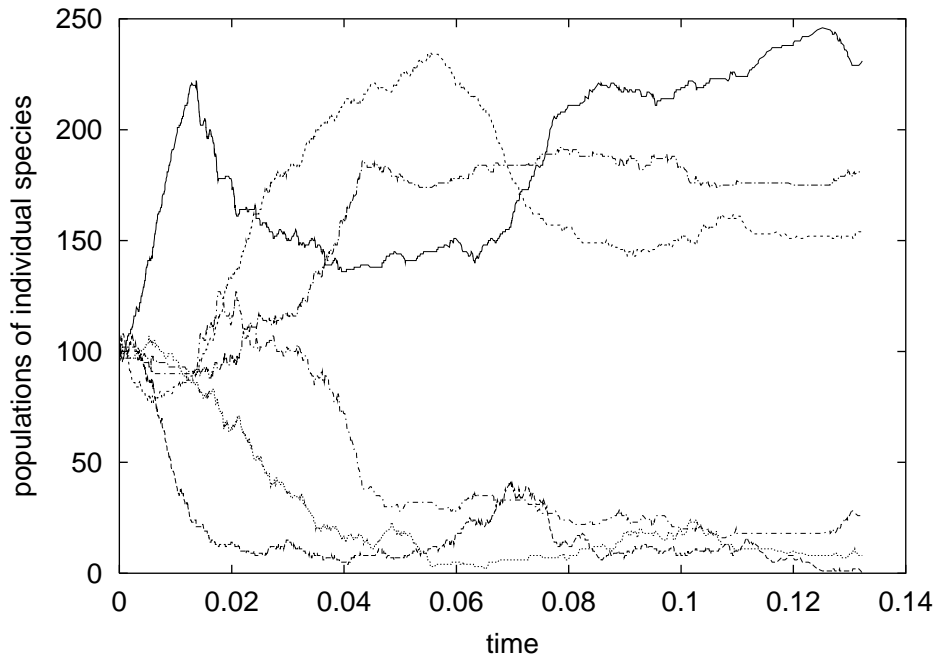


Figure 2: The time series for the six-species system ($N = 600$). All the copies result in a state in which three species (rather than two) survive.

in units of the system size N .

When more species are present in the system, the picture gets more complicated. However, the general feature is that the system experiences “fluctuations-generated forces”, which push the system towards the boundary. There the history of the system ends, since the boundary is absorbing. When the number of species is odd, the population sizes of individual species oscillate with an amplitude that drifts with time, until they reach the boundary, one after another. On the other hand, when the number of species is even, “alliances” do not take long to form, and the history of the system always ends with half of the species winning over the other half. A typical time series for an eight species system is shown in Fig. 3. The fate of the system remains similar throughout the “fixation” regime, i.e. when the diffusion rate $D < 1/N$. In that regime, the system exhibits diffusive behaviour toward the boundary, and the migrations in and out are not frequent enough to bring it back to the centre.

The fluctuations push the neutral system towards the boundary, too, but

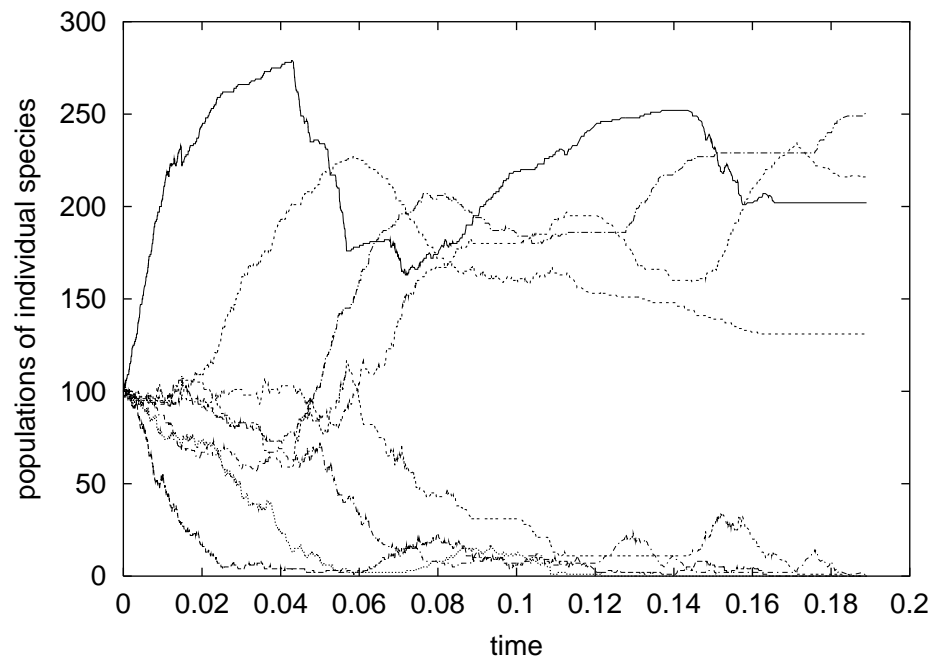


Figure 3: The time series for the eight-species system ($N = 800$). The history of the system ends in a state in which four species survive.

the history of the neutral systems ends either with only one species present, or with disconnected species, in the sense that they have no reason to coexist in symbiosis, since they have no common enemies. On the other hand, the history of the cyclic systems ends with two or more species present. The surviving species do not react with one-another directly, but have common “enemies”. This is quite reminiscent of symbiosis (an alga + a fungus = a lichen, or a tree and mushrooms live together and help each-other fight common enemies), and yet another example of competition giving rise to cooperation.

As a final remark regarding the even-number cyclic system, it is useful to try and “coarse-grain” its dynamics into two species: odd- and even-numbered. For simplicity, let us consider the four-species system. In this case:

$$\begin{aligned} A_{odd} &= A_1 + A_3 \\ A_{even} &= A_2 + A_4 \end{aligned} \tag{17}$$

and the master equation will transform as follows:

$$\begin{aligned} \frac{\partial P(A_{odd}, A_{even}, t)}{\partial t} &= \left\{ \frac{2}{N} \left[(\epsilon_{even} \epsilon_{odd}^{-1} - 1) + (\epsilon_{odd} \epsilon_{even}^{-1} - 1) \right] A_{odd} A_{even} + \right. \\ &+ D \left[(\epsilon_{odd} - 1) A_{odd} + (\epsilon_{even} - 1) A_{even} + \frac{N}{4} (\epsilon_{odd}^{-1} \epsilon_{even}^{-1} - 2) \right] \left. \right\} P(A_{odd}, A_{even}, t) \end{aligned} \tag{18}$$

This is exactly the master equation for Kimura’s two-species neutral drift system [8,9], if we recall that the odd–even system size is $N' = N/2$. Duty has shown that this system is equivalent to a branching process [28] with selection coefficient $s = 0$ [10]. It is critical, and the extinction times scale as \sqrt{N} , and the probability of survival decays with time as t^{-1} , as verified from simulations (see Fig. 4).

It is easy to see that for systems with more species (but always an even number of them) we will obtain the same “coarse-grained” master equation.

6 The Case of Generalized Volterra Equations

Now let us go back to the Volterra equations (3). They can be generalised further, resulting with the following rate equations:

$$\frac{dN_i}{dt} = \sum_j k_{ij} N_j + \frac{1}{N} \sum_{j=1}^n a_{ij} N_i N_j \equiv f_i(N_1, N_2, \dots, N_n) \tag{19}$$

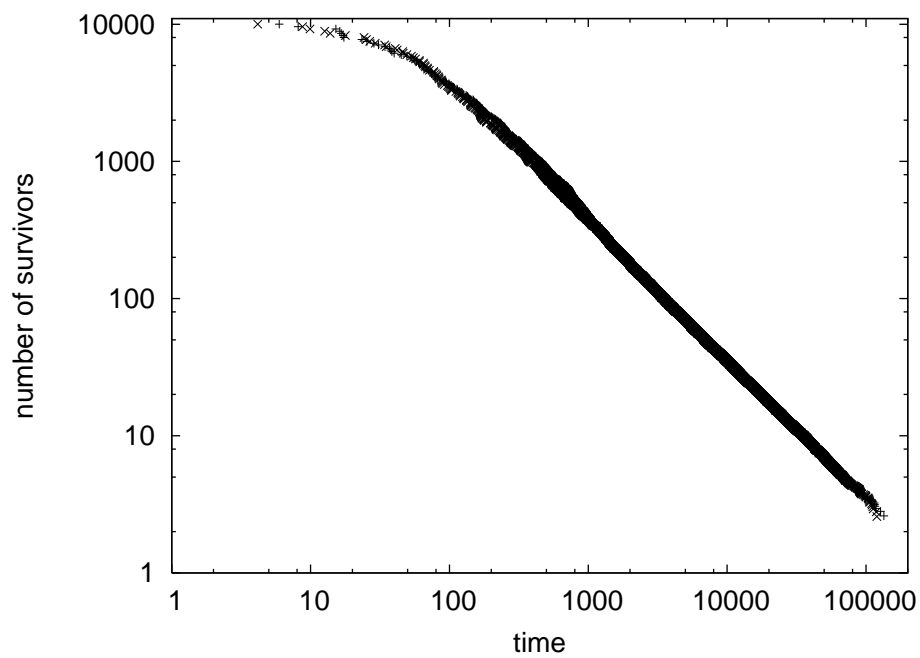


Figure 4: Number of survivors vs. time in log-log axes, for the “coarse-grained” odd-even species, system sizes $N = 4\,000$ and $N = 20\,000$. It maps onto the two-species neutral drift. The slope of the line is -1.03 ± 0.05 for $N = 4\,000$, and -1.006 ± 0.009 for $N = 20\,000$.

where n is the number of species in the system. The diagonal elements in both sums correspond to a Malthus-Verhulst equation. The first sum now contains off-diagonal elements, which correspond to mutations of individuals from species i to species j (or the other way around, depending on the sign of the rate k_{ij} . These mutation rates will be very small.) Hence, the k_{ij} 's and k_{ji} have opposite signs (and also a_{ij} and a_{ji}). The terms of the form $a_{ij}N_iN_j$ describe what happens when an i individual runs into a j individual: when $a_{ij} > 0$ the i individual “eats” a j individual and reproduces, and the other way around when $a_{ij} < 0$. The master equation for the generalised Volterra system, written in terms of the “shift” operators (7):

$$\begin{aligned} \frac{\partial P(\{N_i\}, t)}{\partial t} = \sum_i \left\{ \beta_{ii}(\epsilon_i^{-1} - 1)N_i + \sum_{j \neq i} \beta_{ij}(\epsilon_j \epsilon_i^{-1} - 1)N_j + \right. \\ \left. + \frac{\alpha_{ii}}{N}(\epsilon_i^{-1} - 1)N_i^2 + \sum_{j \neq i} \frac{\alpha_{ij}}{N}(\epsilon_j \epsilon_i^{-1} - 1)N_iN_j \right\} P(\{N_i\}, t) \end{aligned} \quad (20)$$

where the way the master equation is written imposes that the coefficients β_{ij} be chosen as equal to k_{ij} if $k_{ij} > 0$, and zero otherwise. Similarly, $\alpha_{ij} = a_{ij}$ if $a_{ij} > 0$, and zero otherwise.

Now we are ready to attempt the van Kampen expansion of the above master equation. As before, the variables N_i are split into a non-fluctuating and a fluctuating part, as in Eqs. (9), which transforms the probability density function similarly to (10). After substituting everything into the master equation, we obtain a Fokker-Planck equation as in (12), where the A and B matrices have dimensions $n \times n$. The diagonal elements of the A-matrix will be given by $A_{ii} = \beta_{ii} - \sum_{j \neq i} \beta_{ji} + \sum_j (\alpha_{ij} - \alpha_{ji})\phi_j$, and the off-diagonal ones by $A_{ij} = \beta_{ij} - (\alpha_{ij} - \alpha_{ji})\phi_i$. The existence and stability of the solutions to the Volterra equations (3) has been object of extensive studies. When the system is stable, the A-matrix will have negative eigenvalues, which, using the equation (13), will mean that the average value of the fluctuations will decay to zero. Here we are in luck, since, after a careful inspection, we can see that its elements are those of the Jacobian

$$\mathbf{J} = \begin{pmatrix} \frac{\partial f_1}{\partial N_1} & \frac{\partial f_1}{\partial N_2} & \cdots & \frac{\partial f_1}{\partial N_n} \\ \vdots & & & \\ \frac{\partial f_n}{\partial N_1} & \frac{\partial f_n}{\partial N_2} & \cdots & \frac{\partial f_n}{\partial N_n} \end{pmatrix}$$

calculated at the fixed point. If the eigenvalues of this Jacobian are negative, the fixed point is stable. The stability of the solution can be determined

from the *Routh-Hurwitz criteria*. The interested reader can find a treatment of these and further references in Chapter 6 of the book by Pielou [29]. However, the application of Routh–Hurwitz criteria can be tedious and cumbersome, especially when dealing with large systems. The technique of *qualitative stability* helps enormously. It was initiated by the economists Quirk and Rupert [30], and applied to ecological systems by May [31], Levins [32], and Jeffries [33]. See Chapter 6 of the book by Edelstein–Keshet [34] for an extensive review of this subject matter.

The B-matrix has diagonal elements of the form $B_{ii} = \beta_{ii}\phi_i + \sum_{j \neq i} (\beta_{ij}\phi_j + \beta_{ji}\phi_i) + \alpha_{ii}\phi_i^2 + \sum_{j \neq i} (\alpha_{ij} + \alpha_{ji})\phi_i\phi_j$ and off-diagonal ones: $B_{ij} = -\beta_{ij}\phi_j - \beta_{ji}\phi_i - (\alpha_{ij} + \alpha_{ji})\phi_i\phi_j$. They are linear in coefficients β_{ij} and α_{ij} , which means that the equations for the second moments of the fluctuations (obtained from their general expression (14)) will also be linear in the rate coefficients. This will lead to a size-induced transition as the one calculated for the autocatalytic loops, and observed in simulations by us for the three-species systems [12], and Togashi and Kaneko for four-species systems [25, 26].

7 Conclusions

The transition observed by Togashi and Kaneko [25, 26] in the four-species autocatalytic loops is not specific to systems with a very small number of particles/individuals. It is the same critical transition we have previously [12] observed for three-species systems. This transition corresponds to a crossover from a fully symmetric (“neutral”) state in the high-migration regime, to a “fixation” state for low-migration rates, in which the symmetry is broken in favour of one or more species. The “fixation” regime in the four-species system exhibits a symbiosis effect, when species A_1 and A_3 join their efforts against species A_2 and A_4 , and the final state of the system is one in which one of the pairs has completely “eaten up” the other. This transition is present for any finite system size. In the high-migration regime the system allows for a linear noise approximation, exhibiting itself as an Ornstein-Uhlenbeck process.

Since the system size is always finite (no matter how large it is), there is a value of the migration probability per particle (or diffusion rate) for which the fluctuations of the concentrations become of order one, and the system undergoes a critical transition. The critical diffusion rate varies with system size as $1/N$, and the product $DN \sim 1$, i.e. the number of migrants per unit time, necessary for the symmetry to be preserved in the system (all

species to survive) is of the order 1. This result is a bit counterintuitive, since it does not depend on system size. The analytical calculations are in excellent agreement with the simulation results, obtained for three- and four-species systems [12, 25]. Those analytical calculations suggest that all the loop-like autocatalytic systems will exhibit the same critical transition. The form of the equations for the moments of the fluctuations suggests that the generalised Lotka-Volterra systems will also exhibit a similar transition.

This situation, known as diffusion-limited reaction, has manifested itself and been observed in physical systems low dimensions, when diffusion is not efficient in mixing the reactants. A physical example is the Ovchinnikov-Zeldovich segregation phenomenon [35].

In such a situation the hope is that sufficient migration between habitat patches will save the system from extinction. Abta and Shnerb [36] show that the systems in which only the predator is allowed to migrate (such as herbivore-plant or parasite insect-plant systems, like the Prickly Pear cactus and the moth *Cactoblastis cactorum* in Eastern Australia) may support oscillations in noisy environment. Much work is yet to be done in the future.

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