Crossover behaviour of 3-species systems with mutations or migrations

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Abstract. We study the ABC model in the cyclic competition ($A+B \rightarrow 2B$, $B+C \rightarrow 2C$, $C+A \rightarrow 2A$) and the neutral drift ($A+B \rightarrow 2B$ or $2A$, $B+C \rightarrow 2C$ or $2B$, $C+A \rightarrow 2A$ or $2C$) versions, with mutations and migrations introduced into the model. When stochastic phenomena are taken into account, there are three distinct regimes in the model. (i) In the "fixation" regime, the first extinction time scales with the system size N and has an exponential distribution, with an exponent that depends on the mutation/migration probability per particle μ. (ii) In the "diversity" regime, the order parameter remains nonzero for very long times, and becomes zero only rarely, almost never for large system sizes. (iii) In the critical regime, the first passage time for crossing the boundary (one of the populations becoming zero) has a power law distribution with exponent -1. The critical mutation/migration probability scales with system size as N^{-1}. The transition corresponds to a crossover from diffusive behaviour to Gaussian fluctuations about a stable solution. The analytical results are checked against computer simulations of the model.

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1 Introduction

Cyclic phenomena play a very important role in different classes of processes in nature, particularly in epidemiological and ecological systems. In the epidemiological context, examples are diseases which do not leave us with permanent immunity [1,2]. In ecology, cases when three variants of a species compete with one-another in a cyclic fashion have been observed [3–6]. Another system of interest are cyclic food webs. Recently, Kerr et al. obtained laboratory results for a system of three competing species that play rock-paper-scissors, when placed in a lattice-like spatial structure, and showed that there is agreement of the simulation results to the laboratory ones [7]. Its alternative, as far as evolutionary processes are concerned, is the famous Kimura-Weiss model of neutral genetic drift [8,9].

In a previous article [10] we have considered a nonspatial version of the ABC model in both the cyclic competition and neutral genetic drift versions, and studied the evolutionary time behaviour of such a model. 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, i.e. biodiversity is lost. The number of survivors vs. time plots show an exponential decay. It is very interesting to note that there is no difference in the extinction time scale for the ensemble of competing species and the case of neutral drift. This allows us to think of

the neutral model as an "adiabatic approximation" of the cyclic system. Considering that the cyclic competition system would be a minimal model (three alleles) of Darwinian evolution picture, it seems that, by just looking at the results, we can not tell which one must have been the mechanism for the evolution!

There is growing concern about the effects of habitat fragmentation in the survival of a species [11]. Small, isolated forest fragments lose species–we have many examples in the case of fast deforestation worldwide [12]. Some species were lost within a few years of their isolation from the once-continuous forest [13]. Oscillations in the number of population of one "species" are observed in the case of epidemics, as well as ecology. Throughout the past century we have observed changes in patterns of epidemics [14]. For some diseases, the major transitions have been between regular cycles and irregular epidemics, and from regionally synchronized oscillations to complex, spatially incoherent epidemics. Sinervo et al. [5,15] observed spatio-temporal oscillations in the number of lizards (male and female) that employ different mating strategies.

Many population ecologists then conclude that a very important issue is the synchrony of population dynamics in different habitat patches [16–20]. If the population of a certain species goes extinct in one patch while it still survives in other patches, then the hope is that what is known as "rescue effect" can prevent global extinction [17]. Otherwise, the population ecologists say, if there is synchrony of population dynamics between

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patches, the species is doomed to go extinct altogether. In this framework, there have been many proposed strategies for preservation, one of the most debated of which is the construction of "conservation corridors" that would make it possible for individuals to move along habitat patches [21,22].

Considering that each habitat patch can be thought of as one copy of our non-spatial ensemble, it seemed reasonable to study the behaviour of the three-species cyclic system in the presence of mutations or migration. In the following section we introduce our model, and in the next ones, we present the results of our calculations and simulations.

2 The model

Consider a non-spatial (well-stirred) system in which three species A, B, C are competing in a way described by the reactions: $A+B \to 2B$ at a rate AB/N, $B+C \to 2C$, $C+A \to 2A$ at corresponding rates. Add to it the reactions: $A \to B$ at rate μA, $A \to C$ at rate μA, $B \to A$ at rate μB, $B \to C$ at rate μB, $C \to A$ at rate μC, and $C \to B$ at rate μC, where μ is the probability of mutations per individual particle in unit time.

The rate equations for this system will be:

$$\frac{dA}{dt} = \frac{AC}{N} - \frac{AB}{N} + \mu B + \mu C - 2\mu A$$
$$\frac{dB}{dt} = \frac{BA}{N} - \frac{BC}{N} + \mu A + \mu C - 2\mu B \qquad (1)$$
$$\frac{dC}{dt} = \frac{CB}{N} - \frac{CA}{N} + \mu A + \mu B - 2\mu C$$

with $A+B+C = N = $ const. If the neutral drift system is considered instead, i.e. when $A+B \to 2A$ or $2B$ with equal probability (and similarly for the two other reactions), the rate equations will only contain the terms that depend on μ, and the first two terms will be absent.

In another version, mutations are replaced by migration into and out of the "island". In other words, the following migrations are happening: A out at rate $3\mu A$, B out at rate $3\mu B$, C out at rate $3\mu C$, A, B, or C in at constant rate $\mu \cdot N$, where N is the system size (to make it comparable to the rate of leaving the island. This would correspond to the average number of individuals in other patches, which are the source of our "immigrants".) The rate equations will be the same as those for the system with mutations. The above equations have a fixed point at $A = B = C = N/3$, and it is a stable solution.

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 get the correct picture of the evolution of the system. For that we ought to write the master equation, and then try to somehow expand it, obtaining a Fokker-Planck equation, and eventually solve it. The two most commonly

used expansions of the master equation are the Kramers-Moyal expansion, which is essentially a Taylor expansion in powers of system size N, and the Ω-expansion of van Kampen [23] which is an expansion in powers of $\sqrt{N}$. The first method produces a nonlinear Fokker-Planck equation. The second method is quite systematic, and yields satisfactory results when the system has a single stable point, as the rate equations suggest is the case with the present model. In the absence of this stable solution, the task becomes very difficult [10].

Using the "shift" operators notation:

$$\epsilon_A f(A, B, C) = f(A+1, B, C)$$
$$\epsilon_A^{-1} f(A, B, C) = f(A-1, B, C)$$

the master equation for the cyclic competition system with mutations reads:

$$\frac{\partial P(A, B, C, t)}{\partial t} = \left\{ \frac{1}{N} \left[(\epsilon_C \epsilon_A^{-1} - 1)AC + (\epsilon_A \epsilon_B^{-1} - 1)AB \right. \right.$$
$$\left. + (\epsilon_B \epsilon_C^{-1} - 1)BC \right] + \mu \left[(\epsilon_A \epsilon_B^{-1} + \epsilon_A \epsilon_C^{-1} - 2)A \right.$$
$$\left. \left. + (\epsilon_B \epsilon_C^{-1} + \epsilon_B \epsilon_A^{-1} - 2)B + (\epsilon_C \epsilon_A^{-1} + \epsilon_C \epsilon_B^{-1} - 2)C \right] \right\}$$
$$\times P(A, B, C, t) \quad (2)$$

while that for the neutral drift system with mutations:

$$\frac{\partial P(A, B, C, t)}{\partial t} = \left\{ \frac{1}{2N} \left[(\epsilon_C \epsilon_A^{-1} + \epsilon_A \epsilon_C^{-1} - 2)AC \right. \right.$$
$$\left. + (\epsilon_A \epsilon_B^{-1} + \epsilon_B \epsilon_A^{-1} - 2)AB + (\epsilon_B \epsilon_C^{-1} + \epsilon_C \epsilon_B^{-1} - 2)BC \right]$$
$$+ \mu \left[(\epsilon_A \epsilon_B^{-1} + \epsilon_A \epsilon_C^{-1} - 2)A + (\epsilon_B \epsilon_C^{-1} + \epsilon_B \epsilon_A^{-1} - 2)B \right.$$
$$\left. \left. + (\epsilon_C \epsilon_A^{-1} + \epsilon_C \epsilon_B^{-1} - 2)C \right] \right\} P(A, B, C, t) \quad (3)$$

and that for the cyclic system with migrations:

$$\frac{\partial P(A, B, C, t)}{\partial t} = \left\{ \frac{1}{N} \left[(\epsilon_C \epsilon_A^{-1} - 1)AC + (\epsilon_A \epsilon_B^{-1} - 1)AB \right. \right.$$
$$\left. + (\epsilon_B \epsilon_C^{-1} - 1)BC \right]$$
$$+ 3\mu \left[(\epsilon_A - 1)A + (\epsilon_B - 1)B + (\epsilon_C - 1)C \right.$$
$$\left. \left. + \frac{N}{3}(\epsilon_A^{-1} + \epsilon_B^{-1} + \epsilon_C^{-1} - 3) \right] \right\} P(A, B, C, t). \quad (4)$$

3 The "fixation" regime

In a previous work [10] we studied the cyclic competition and neutral genetic drift systems in absence of mutations. In the mean-field approximation (rate equations) the cyclic system has an infinity of neutrally stable solutions: any trajectory that conserves the integral $H = ABC/N^3$ is a stable trajectory of the system. On the other hand, the neutral drift system has an infinity of neutrally stable points: any state of the system is stable in the mean-field picture. The story is different, when stochastic birth-and-death processes are taken into account: then the individual population distribution drifts, until one of the
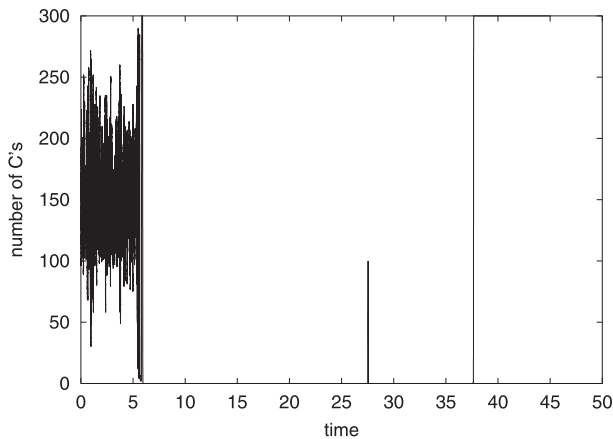
Fig. 1. The time series for the number of C species in the "fixation" regime (here $\mu = 0.4 \times 10^{-3}$, and system size $N = 300$).

Fig. 2. Dependence of the exponent of the decay of the survival probability on the mutation rate in the "extinction" regime for system size $N = 150$.

species, and then another one, go extinct. In other words, there is fixation of the population to one of the varieties, and the product $H = ABC/N^3$ becomes zero. The survival probability versus time (in units of N) plot exhibits exponential decay with slope -3, which was verified by numerically solving the corresponding Fokker-Planck equation. This equation was obtained from a Kramers-Moyal expansion, since the infinite multiplicity of stable solutions (points or limit cycles) makes the van Kampen method impractical to apply. The first extinction time scales with the total population size N. This behaviour is the same for both the cyclic competition and the neutral drift models, the second one behaving as an "adiabatic approximation" to the first one. For both models, the probability distribution function becomes uniform within a short time, i.e. any point inside the triangle that represents the phase space of the system is equally probable.

When μ is small (the meaning of small will become clear in Sect. 5) the system with mutations/migrations is in the "fixation" regime, in which the results of our previous study [10] are applicable qualitatively. In that regime, the stochastic processes push the system towards the (absorbing) boundary, in which at least one of the species has met extinction. This was verified by computer simulations of the master equations (2, 3, 4). These simulations started with equal individual populations of A, B, C, (i.e. the centre). We generated times for the next possible reaction event with exponential distribution as $-\frac{\ln(rn)}{rate}$, where the rate of the cyclic/neutral or mutations/migrations as in the master equations above (2, 3, 4) is substituted. (Here rn is a random variable with uniform distribution in $[0, 1]$. This way we get Poisson distribution for the event times, i.e. really independent events [24].) 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 a "fixation" regime, in which one of the populations, and then the next one, go to zero quite fast. In this regime, the number of individual populations oscillates with an amplitude that drifts with time. The main reaction is then the cyclic one, and there are only
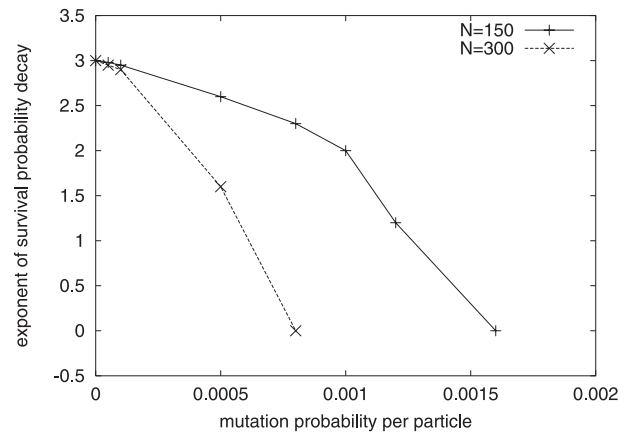
occasional mutations/migrations, which are not frequent enough to prevent fixation. In other words, the system is experiencing "forces" due to fluctuations, and "forces" due to mutations (migrations). The fluctuations are pushing the system toward the boundary, while the mutations (migrations) push toward the centre. For small mutation/migration rate the "fluctuation-generated forces" are stronger. Figure 1 shows the variation with time of the population of C's for a realisation of the system in the "extinction" regime. Occasionally, an individual of the competing species (the one next in the "food chain") is introduced in the system by mutations (or migrations), and then it either causes an occasional spike in the time series (like the one we see in Fig. 1 at $25 < t < 30$, or it "eats up" the old species completely and replaces it in the system (which is what happens between $t = 35$ and $t = 40$ in our plot).

We investigated the behaviour of the probability distribution for the first crossing of the boundary, i.e. when one of the populations becomes zero for the first time, as the mutation/migration rate increases. For that we ran ten thousand copies of the system for each value of the mutation rate. The survival probability (as defined above) was plotted vs. time. In the "fixation regime" the decay is still exponential, but the exponent varies with the mutation/migration rate, getting close to zero as the system approaches criticality. Figure 2 shows a plot of the exponent as a function of mutation probability μ for system size $N = 150$ and $N = 300$.

4 The "diversity" regime

If only mutations (migrations) are present, the system remains near the centre point ($A = B = C = N/3$), and the order parameter remains considerably above zero; in other words, all three species are present in the system. One can occasionally observe temporary extinctions, but this happens very seldom, and for very long times; when the system size is very large, it almost never happens. Since the boundary is not absorbing, occasional

mutations/migrations will return the system to the state with maximal symmetry (biodiversity) where all three varieties coexist. When both the cyclic/neutral drift mechanism and mutations (migrations) are present, and the μ is above critical, the mutations manage to keep the system maximally disordered, since they are stronger than the fluctuations (which, as we saw, try to drive the system toward the boundary, i.e. fixation, and keep it there). Compared to the situation with no/low mutations (migrations), where the boundary is (practically) absorbing, and the final state of the system is a "pure" one (with only one of the species present), the mutation/migration rate acts then as a "temperature".

Work has been done on the two allele almost neutral drift model with mutations [25]. 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 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 the 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 point 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 first-order, and critical behaviour is observed. The system behaves similarly when migrations are present, instead of mutations. One aspect of migrations in a four-species system has been treated recently by Togashi and Kaneko [26].

Since the rate equations have a stable solution, we employ the van Kampen expansion [23]. The idea of this expansion 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. In this approach, the numbers of the individual populations would be written as:

$$A = N\phi_1 + \sqrt{N}x_1$$
$$B = N\phi_2 + \sqrt{N}x_2 \qquad (5)$$
$$C = N\phi_3 + \sqrt{N}x_3.$$

Here the ϕ_i are the concentrations of A, B, and C species respectively (which only depend on time), and the x_i are the fluctuations (proportional to the square root of system size). The system size (total population) N is conserved for the system with mutations, but not for that with migrations. This conservation rule will cause trouble in the case of the system with mutations, and will require special attention. Using the van Kampen Ansatz, the probability distribution $P(A, B, C, t)$ is transformed into $\Pi(\{x_i\}, t)$,

and the following relations are true:

$$\Pi = N^{3/2}P\left(N\left\{\phi_i + \sqrt{N}x_i\right\}, t\right)$$
$$\frac{\partial P}{\partial t} = \frac{1}{N^{3/2}}\frac{\partial \Pi}{\partial t} - \frac{1}{N}\sum \frac{d\phi_i}{dt}\frac{\partial \Pi}{\partial x_i}$$

and

$$\epsilon_i = 1 + \frac{1}{\sqrt{N}}\frac{\partial}{\partial x_i} + \frac{1}{2N}\frac{\partial^2}{\partial x_i{}^2} + \dots$$
$$\epsilon_i{}^{-1} = 1 - \frac{1}{\sqrt{N}}\frac{\partial}{\partial x_i} + \frac{1}{2N}\frac{\partial^2}{\partial x_i{}^2} + \dots \qquad (6)$$

Next we substitute everything into the master equation, leave only the term $\partial \Pi/\partial t$ in 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 for e.g. the cyclic model is:

$$\sum \frac{\partial \Pi}{\partial x_i}\left[\frac{d\phi_i}{dt} + \phi_i\phi_{i+1} - \phi_i\phi_{i+2}\right.$$
$$\left. + \mu(2\phi_1 - \phi_{i+1} - \phi_{i+2})\right] = 0, \qquad (7)$$

which reproduces the rate equations in terms of the concentrations ϕ_i, with steady state solution $\phi_i = 1/3$. Similarly, we get the rate equations for the other models.

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

$$\frac{\partial \Pi}{\partial t} = \sum\left[-A_{ik}\frac{\partial}{\partial x_i}(x_k\Pi) + \frac{1}{2}B_{ik}\frac{\partial^2 \Pi}{\partial x_i\partial x_k}\right]. \qquad (8)$$

4.1 The system with migrations

We are going to solve the system with migrations first, since the absence of the conservation of total population N makes this system easier to deal with. For simplicity, let us limit our attention to fluctuations around the steady state $\phi_i = 1/3$. The A-matrix for the system with migrations is:

$$\begin{pmatrix} -3\mu & -1/3 & 1/3 \\ 1/3 & -3\mu & -1/3 \\ -1/3 & 1/3 & -3\mu \end{pmatrix}$$

and the B-matrix:

$$\begin{pmatrix} 2\mu + 2/9 & -1/9 & -1/9 \\ -1/9 & 2\mu + 2/9 & -1/9 \\ -1/9 & -1/9 & 2\mu + 2/9 \end{pmatrix}.$$

These equations are linear, and the coefficients depend on time through ϕ_i. 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
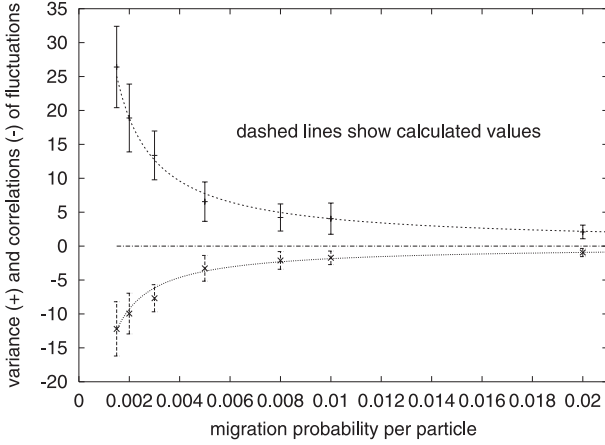
Fig. 3. The variance and correlations of the fluctuations vs. migration probability per particle for system size $N = 300$, cyclic system. The same behaviour is observed for the system with mutations.

to determine the first and second moments of the fluctuations. Following van Kampen [23], we can multiply the Fokker-Planck equation by x_i and integrate by parts to get:

$$\frac{d\langle x_i\rangle}{dt} = \sum_j A_{ij}\langle x_j\rangle. \tag{9}$$

The eigenvalues of the A matrix are of the form -3μ, $-3\mu \pm i/\sqrt{3}$. 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:

$$\frac{d\langle x_i x_j\rangle}{dt} = \sum_k A_{ik}\langle x_k x_j\rangle + \sum_k A_{jk}\langle x_i x_k\rangle + B_{ij}. \tag{10}$$

By symmetry, in the steady state 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 μ alone. The steady state solutions are:

$$\langle x_i^2\rangle = \frac{9\mu+1}{27\mu} \tag{11}$$

$$\langle x_i x_j\rangle = -\frac{1}{54\mu}.$$

The diagonal terms coincide with the variance, since the $\langle x_i\rangle = 0$. These fluctuations were measured "experimentally", i.e. calculated from the results of the simulations. We simulated 1000 copies of the system (size $N = 300$) at different mutation rates, and calculated the mean and variance of the fluctuations, as well as correlations. The results of those simulations are shown in Figure 3 for the system with migrations. They agree with the calculated values.

4.2 The system with mutations

In the case of the system with mutations, the total population N is a conserved quantity; this imposes restrictions on

allowed fluctuations. We avoid this problem by excluding one of the variables. For that, we transform the problem into one with two variables, which can be done by putting:

$$\frac{A}{N} = \frac{1}{3} - \frac{1}{\sqrt{N}}\left(\frac{\sqrt{3}}{2}x + \frac{y}{2}\right)$$

$$\frac{B}{N} = \frac{1}{3} + \frac{1}{\sqrt{N}}\left(\frac{\sqrt{3}}{2}x - \frac{y}{2}\right) \tag{12}$$

$$\frac{C}{N} = \frac{1}{3} + \frac{y}{\sqrt{N}}.$$

This corresponds to transforming to Cartesian coordinates with the origin placed at the geometrical centre of the equilateral triangle, which constitutes the phase space of our system [10].

The Fokker-Planck equation for the cyclic competition system becomes:

$$\frac{\partial\Pi}{\partial t} = \frac{\partial}{\partial x}\left(\frac{y}{\sqrt{3}} + 3\mu x\right)\Pi - \frac{\partial}{\partial y}\left(\frac{x}{\sqrt{3}} - 3\mu y\right)\Pi$$
$$+ \frac{1+6\mu}{9}\left(\frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}\right)\Pi. \tag{13}$$

The A-matrix has the form:

$$\begin{pmatrix} -3\mu & -1/\sqrt{3} \\ 1/\sqrt{3} & -3\mu \end{pmatrix}$$

with eigenvalues $-3\mu \pm i/\sqrt{3}$. The mean value of the fluctuations decays to zero with an oscillating behaviour, and remains zero. The B-matrix is diagonal, with both diagonal elements equal to $\frac{2}{9}(1+6\mu)$. The equations for the second moments become:

$$\frac{d\langle x^2\rangle}{dt} = -6\mu\langle x^2\rangle - \frac{2}{\sqrt{3}}\langle xy\rangle + \frac{2}{9}(1+6\mu)$$

$$\frac{d\langle xy\rangle}{dt} = \frac{2}{\sqrt{3}}\langle x^2\rangle - 6\mu\langle xy\rangle - \frac{2}{\sqrt{3}}\langle y^2\rangle \tag{14}$$

$$\frac{d\langle y^2\rangle}{dt} = \frac{2}{\sqrt{3}}\langle xy\rangle - 6\mu\langle y^2\rangle + \frac{2}{9}(1+6\mu)$$

with solutions that tend to

$$\langle x^2\rangle = \langle y^2\rangle = \frac{1+6\mu}{27\mu}, \quad \langle xy\rangle = 0 \tag{15}$$

as $t \to \infty$. These solutions need to be transformed back in terms of $\langle x_i^2\rangle$ and $\langle x_i x_j\rangle$, and the results are:

$$\langle x_i^2\rangle = \frac{1+6\mu}{27\mu} \tag{16}$$

$$\langle x_i x_j\rangle = -\frac{1+6\mu}{54\mu}.$$

For the neutral drift case, the Fokker-Planck equation becomes:

$$\frac{\partial\Pi}{\partial t} = \frac{\partial}{\partial x}(6\mu x\Pi) + \frac{\partial}{\partial y}(6\mu y\Pi)$$
$$+ \frac{2(1+6\mu)}{9}\left(\frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}\right)\Pi \tag{17}$$

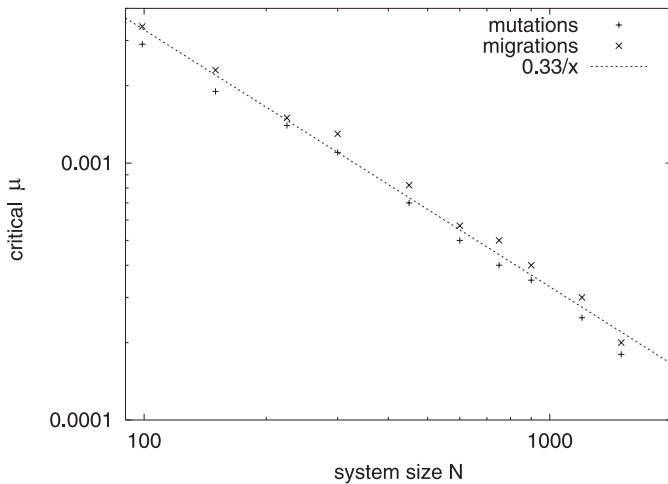**Fig. 4.** Variation of critical mutation and migration probability per particle with system size.

Fig. 5. Cumulative survival probability vs. time (in units of N) just below, just above, and at the critical point, cyclic system with mutations, system size $N = 210$.

with the same steady state distributions as the cyclic competition model.

5 The transition region

The qualitative change in the behaviour of the system, when the value of the parameter μ is varied, speaks of the presence of a phase transition. The survival probability decays exponentially with time in the "fixation" regime, and the exponent goes down as the mutation probability increases, as shown in Figure 2. This speaks of a symmetry-breaking transition as the mutation probability goes through the critical value.

When the mutation/migration probabilities per particle approach zero, the leading term in the variances of the concentrations of individual populations is of order $1/27N\mu$, and it becomes of the same order of magnitude as the macroscopic concentrations, when $3\mu N \propto 1$. This gives us the critical mutation/migration probability dependence on the system size N. The critical μ was verified to be the same for both models with mutations present, and the critical μ for the system with migrations from the simulations is very close to that for the systems with mutations, which supports the calculations above. Figure 4 shows plots of critical μ vs. N, as well as a line of slope $1/N$ for comparison. To further verify this result, we performed a Kramers-Moyal expansion the models with mutations and migrations, in which μ was posed as μ_0/N. Numerical solution of the resulting nonlinear Fokker-Planck equations gave the equation for the eigenvalue (exponent of decay): $\lambda = 9\mu_0 - 3$, where λ is the eigenvalue. At criticality, $\lambda = 0$, which yields $\mu_0 = 1/3$ or $\mu = 1/3N$ [27]. This is in excellent agreement with the results obtained from the analysis above, as well as the computer simulations. It is worth noting that the neutral system essentially behaves like the cyclic one.

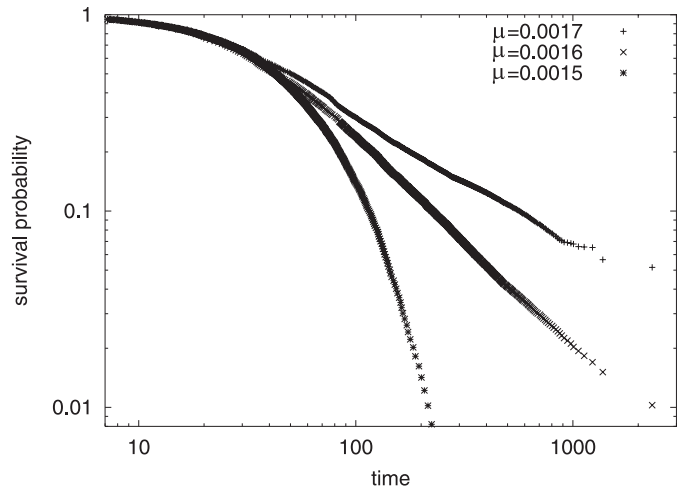The probability that the system has never crossed the boundary, (i.e. none of the populations has ever become

zero), when the system is in the transition regime, still decays to zero, but not exponentially any more. The transition is critical; however, transitions in nonequilibrium (steady-state) systems are different from the thermodynamic phase transitions. If the system size were infinite, one would introduce one infected individual (mutant) and measure the probability of survival of infection/mutation as time goes to infinity. This would constitute the order parameter of our system in the thermodynamic limit. However, our systems are finite, and for finite N the quantity which exhibits critical behaviour is the first passage time for crossing the boundary[1].

In Figure 5 we show plots of the first extinction times (with their cumulative probability in the y-axis) just below, just above, and at the critical μ (system size $N = 210$). (It is worth mentioning that we ran a statistics of 10000 copies of the system, but we are showing only 1 in 20 points in that plot, to prevent figures from becoming cluttered.) The power-law decay behaviour was used as a criterion for determining the critical point. The plot in Figure 5 shows clearly that the survival probability decays as a power law at the critical point. However, once the system is above the critical point, there is considerable probability for the system to have never "gone dead", even at very long times. The extinction times at the critical point scale with the system size. The power-law exponent is -1.03 ± 0.04 for cyclic competition model, -0.99 ± 0.03 for the neutral model with mutations; and -1.05 ± 0.06 for the cyclic system with migrations. This exponent close

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[1] Our model differs from the chemical reactions models: in them the onset of the cyclic behaviour is a Hopf bifurcation, in which a stable focus changes into a limit cycle [28]. In our model the limit cycle is absent. The chemical reactions models are dissipative even in the mean-field approximation, while our system has a centre in the mean field treatment. In those models the fluctuations become important only when the system is in the vicinity of the Hopf bifurcation, ours is entirely fluctuations-driven below the critical transition point.

to 1, found in simulations is compatible with the one expected from branching processes [29], as well as the one obtained for the two-species Kimura-Weiss model [25].

6 Conclusions

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 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, i.e. the order parameter, defined as the product of ABC/N^3 goes to zero, and remains zero, except for occasional "bursts". In the "diversity" regime, the number of the A, B, C varieties fluctuates around the centre point, and there are rare extinctions, but the order parameter 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 N^{-1}, and the models have the same power-law exponent: -1. There is no difference in the behaviours of the neutral system and the cyclic system. Also, there is no qualitative difference between the system with mutations and that with migrations.

These results address the concern about the effects of habitat fragmentation in the survival of the species [11]. If the population of a certain species goes extinct in one patch (e.g. a herd, school, swarm) while it still survives in other patches, then it is hoped that the "rescue effect" can prevent global extinction [16–18]. Otherwise, the species is doomed to go extinct altogether. Our results suggest that the number of mutants/migrants necessary to preserve diversity is independent of system size, while in most realistic situations the number of mutations that happen would be proportional to system size. On the other hand, if one has in mind epidemiological systems, the important factor is to reduce migration probabilities below critical, which is exactly the purpose quarantines serve. Let's recall here the revival of SARS epidemics in Toronto, once the guard was let down, i.e. infected individuals were allowed to migrate from one community on to others. In that case, a large system size may be a disadvantage. It takes only one bad apple...

In lattice models [30,31] small amounts of migration bring about "phase synchronization". Peak population abundances, however, are observed to be largely uncorrelated. Blasius et al. [17] use a Langevin type system of equations to introduce noise in the three-species spatially structured model, and obtain complex chaotic travelling-wave structures.

This work on three-species ecological or epidemiological systems relates to autocatalytic systems with a loop-like structure [26,32]. Methods of analysis employed in this paper can be expanded to the loop-like autocatalytic systems. We have work in progress regarding the four- or more-species autocatalytic loops [33].

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