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Symmetry of interactions rules in incompletely connected random replicator ecosystems

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Abstract. The evolution of an incompletely connected system of species with speciation and extinction is investigated in terms of random replicators. It is found that evolving random replicator systems with speciation do become large and complex, depending on speciation parameters. Antisymmetric interactions result in large systems, whereas systems with symmetric interactions remain small. A co-dominating feature is within-species interaction pressure: large within-species interaction increases species diversity. Average fitness evolves in all systems, however symmetry and connectivity evolve in small systems only. Newcomers get extinct almost immediately in symmetric systems. The distribution in species lifetimes is determined for antisymmetric systems. The replicator systems investigated do not show any sign of self-organized criticality. The generalized Lotka-Volterra system is shown to be a tedious way of implementing the replicator system.

1 Introduction

In the light of fossil records, the evolution of species may appear to be a self-organized critical phenomenon, the size distribution of extinction events possibly following a power-law [1–5]. The evolution of species can possibly be described in terms of a *punctuated equilibrium*: the system of life becomes settled into a stasis, which then becomes disturbed by species appearances and avalanches of extinctions. Consequently, the development of species appears to miss continuity [6,1,3,7]. A dramatic avalanche of extinction often is followed by rapid recovery [3,4].

A variety of computational approaches has been used in order to investigate the evolution of life [8–10]. The model by Bak and Sneppen [11,12,5], appears to self-arrange into a critical state. Models of catalytic networks containing a definite number of species show many of the features observed in the paleontological records [13–19]. A possibly more realistic evolution model with hierarchical ecosystems, on the other hand, does not appear to produce large avalanches of extinctions [20–22]. A self-organized extinction dynamics is can be reproduced for a system with a predetermined number of species [23,24]. A model like this of course does not give any insight into how such a species system evolves in the first place.

A statistically stationary system by definition has constant long-term average properties. In the case of a stationary system of life, having passed its initial transient state, species extinctions must be related to the appearance of new species. Marine life on earth appears to have been in such an apparently stationary state for most of the last 500 million years [4]. The Bak-Sneppen model retains the number of living species, and thus corresponds to a stationary system [11,12,5]. Within the tree-like model by Vandewalle and Ausloos [25,26], the number of living species increases continuously. The model might be modified to describe a stationary system by introducing additional species extinctions [27].

One of the most functional ways of modelling ecological systems is the use of replicator equations. Replicators refer to systems where a configuration of "strategies" or "species" contributes to the "fitness" or "payoff" of any particular strategy. The "fitness" or "payoff" in turn contributes to the concentration of each "strategy" or "species". An important contrast with the catalytic network model is that the fitness regulates concentration in relation to the existing concentration. In other words, within the replicator model, parents of the same species are needed.

Recently, quenched random replicator systems have been investigated analytically at the limit of a large number of interacting species [28–32]. Species richness is reported to increase along with reduced symmetry of interactions, as well as with increased within-species interaction pressure [28,32].

Attempts to directly apply random replicator models in investigations into the evolution of life have either not produced large, complex ecosystems, or have not resulted in large, recovering avalanches of extinctions, depending on the parameters used [16,21,33]. This may be due to the

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region of parameter space investigated not corresponding to that appearing in reality. New species as immigrants unrelated to previous species, with fully connected networks and initially asymmetric interactions, have resulted in small systems only [33]. Another case with fully connected, initially asymmetric networks but without within-species interaction also has resulted in ecosystems of just a few species [34].

None of the references discussed above explicitly discusses spatial distribution of species. At first glance, this appears as a significant shortcoming. Speciation obviously is intimately related to segregation. Segregation, however, does not need to be spatial, it may be temporal [35,36]. Details of segregation mechanisms have been neglected in the references above, and speciation has instead been treated as kind of a random process. The present author agrees with such a view and does not discuss the details of segregation mechanisms.

Spatial distribution indeed does not only affect speciation but also species co-evolution and the consequent extinctions. In other words, spatial distribution certainly affects species interactions. However, a variety of factors affect the interaction of species. It hardly is feasible to explicitly consider all such factors. In the mind of the author, this justifies the representation of species interaction as a random process. The randomness of species interactions is here implemented in two ways. Firstly, species are incompletely connected, nonzero interaction coefficients being randomly assigned and subject to evolution along with speciations and species extinctions. Secondly, the magnitude of the nonzero interaction coefficients is randomly assigned, and also subject to evolution along with speciations and species extinctions.

System states where observables are scale-free have been interpreted as critical [37–42]. The origin of the nomenclature obviously is in phase transitions at a few particular "critical points" [37,38,42]. In other words, critical systems show fractal properties, observables being distributed according to power-laws [37,38,40,43,39,42]. However, power-law distributed observables may appear simply as a result of a random process, and do not necessarily imply criticality [44,42]. Power-law distributed observables however are a necessary condition for criticality [44].

Not all systems self-organize to critical points. Scale-free behaviour may be found simply by tuning system parameters towards a critical phase transition. It obviously is disputable whether or not self-organized criticality is a phenomenon characteristic to wide variety of complex systems in Nature [8,37–39,41,37,5,42].

We intend to find out whether random replicator systems with speciation produce large, complex systems, and how does this possibly depend on parameters of the system. First, we introduce a within-species interaction. Second, we consider interaction matrices not fully connected. To us, a fully connected ecosystem appears as a rather unrealistic assumption. Thirdly, the interactions initiated among species may be partially symmetric or antisymmetric. Naturally, interaction matrix connectivity and symmetry, both having random components, may evolve along with speciations and co-evolutionary processes which lead to species extinctions. We are also interested in eventual signs of criticality in the systems, either self-organized or fixed-point criticality, possibly resulting as power-law distributed observables, lacking any characteristic size scale.

In the remaining part of this paper, we will first introduce our mathematical model. Then, we will investigate the effect of the relative magnitude of within-species interaction, as well as initial symmetry and connectivity in among-species interaction on the model outcome. We will apply three values of initial species connectivity (1, 0.1 and 0.01) and five values of initial symmetry of interactions (-1, -0.5, 0, 0.5 and 1). The within-species interaction will be either equal to or five times the standard deviation of the among-species interaction coefficients. We will first investigate species diversity. Then, eventual evolution of connectivity, symmetry of interactions, and average fitness, will be clarified. Distribution of species lifetime, as well as that of the number of living species will be investigated. Finally, the replicator systems will be converted to generalized Lotka-Volterra systems, and the effect of such a conversion on symmetry, as well as the relative magnitude of among-species interaction, will be clarified.

2 Mathematical model

We start by creating a species configuration vector of two species, one species of unit concentration, and another with a small concentration at an extinction limit of 0.001. (The choice of this numerical value affects the absolute size of the ecosystems, as will be discussed at the end of the paper. The sum of concentrations defined this way generally exceeds unity. Fractional concentration can be produced in a straightforward manner.) Then we create a random square interaction matrix of dimension two, matrix elements drawn from a Gaussian distribution with zero mean and unit variance. The diagonal of the matrix is then replaced by the negative of a within-species interaction pressure u of predetermined mean value and 20% standard deviation. According to predetermined interaction matrix connectivity, randomly determined non-diagonal matrix elements are replaced by vacancies. Connectivity simply refers to appearance probability of a nonzero non-diagonal interaction coefficient. Vacancies are symmetric with respect to the matrix diagonal.

The interaction matrix produced this way corresponds to the asymmetric case. In other words, non-diagonal interaction coefficients Z_{ij} and Z_{ji} have zero covariance. In order to introduce either symmetry or antisymmetry, some amount of covariance must be induced. This is implemented by replacing Z_{ij} and Z_{ji}, for $i < j$, with

$$J_{ij} = Z_{ij}, \quad J_{ji} = \Gamma Z_{ij} + \sqrt{1 - \Gamma^2} Z_{ji}, \tag{1}$$

where Γ refers to a symmetry parameter with values between unity and negative unity, the value zero corresponding to the asymmetric interactions. Correspondingly, J_{ij} and J_{ji} refer to non-diagonal interaction coefficients with possibly some covariance.

The fitness vector is then produced as the product of the interaction matrix and the configuration vector $\boldsymbol{x}$, or equivalently

$$F_i = \frac{1}{\sum x}\left(\sum_{i \neq j} J_{ij} x_j - u x_i\right). \tag{2}$$

Any species concentration is then assumed to change according to the replicator equation

$$\Delta x_i = x_i \left(F_i - \frac{x \cdot F}{\sum x}\right), \tag{3}$$

which can be rearranged as

$$\frac{\Delta x_i}{x_i} = F_i - \overline{F}. \tag{4}$$

Repeated index does not imply summation in eqs. (3) and (4).

Equations (2) and (4) are then applied repeatedly until an equilibrium species configuration is found. The species configuration vector is then inspected, and species with concentrations below the extinction limit are removed. Also the interaction matrix elements corresponding to extinct species are removed. The extinctions naturally change the dimensionality of the concentration vector and the interaction matrix.

Then, the dimensionality of the species configuration vector, as well as the corresponding square interaction matrix is increased by one, the concentration of the new species taken at the extinction limit. The interaction matrix elements for the new species are created according to the procedure explained above. In other words, a column and a row are added to the pre-existing interaction matrix, the matrix elements drawn from a Gaussian distribution with zero mean and unit variance. The diagonal element is then replaced by the negative of a within-species interaction pressure u of predetermined mean value and 20% standard deviation. According to the predetermined interaction matrix connectivity, randomly determined column elements are replaced by vacancies, and the corresponding row elements also replaced by vacancies in order to make the vacancies symmetric. Some amount of symmetry or antisymmetry is introduced according to eq. (1).

Then, eqs. (2) and (4) are applied repeatedly again, and extinctions inspected. Extinct species are removed from the species configuration vector, and their interaction coefficients from the interaction matrix. Then, another new species is introduced, equilibrium concentrations explored, and consequent extinctions identified. The speciation, along with consequent extinctions, is repeated a predetermined number of times.

The solution of the finite difference equations (2) and (4) is required to proceed smoothly. In other words, overly large steps in the iteration must be avoided. The smoothness requirement results from the concentration changes computed here being due to species interaction, instead of catastrophes like meteorites or volcano eruptions. Any step is first reduced by multiplying eq. (4) by 0.1. Regardless of this, there is a possibility of premature extinction due to $\frac{\Delta x_i}{x_i} \leq -1$. It was avoided by inspecting any value of $\frac{\Delta x_i}{x_i}$, and in the case of $\min(\frac{\Delta x_i}{x_i}) \equiv a \leq -1$, reducing the size of that particular iteration step by multiplying eq. (4) by $\frac{-1}{2a}$.

The distribution of species survival times in terms of speciations was determined using a mean-field approximation. At the end of any numerical experiment, the probability density function of extinctions as a function of relative position within the species configuration vector was clarified. Then, an approximation of species survival time was computed for any extinct species as the sum of the number of living and extinct species speciated after the very species, the latter being produced using the probability density function of extinctions.

It is worth noting that eq. (4) is invariant to any translation of fitness values. It was verified that the results are not sensitive to small changes in connectivity and within-species interaction pressure. In addition, replicator dynamics is invariant to affine transformations of the fitness function, modulo change in time scale [45,46]. In the case of discrete-step solutions, the system trajectory however may change. There also is a possibility that several equilibrium species configurations exist. We naturally accept the first equilibrium which is found.

3 Species diversity

In accordance with previous observations [33,34], fully connected systems remained small. However, in the case of the larger within-species interaction pressure, the antisymmetric systems exceeded the size of 100, and even halfly antisymmetric systems were of size of about 40.

Antisymmetric systems with initial connectivity 0.1 were large and stable, of size exceeding 1000 species. In the case of the larger within-species interaction pressure, even halfly antisymmetric systems were of size about 1000. Symmetric and halfly symmetric systems were small, less than 40 species. In the case of the smaller within-species interaction pressure they varied apparently randomly. An asymmetric system in the case of the larger within-species interaction pressure fluctuated in size between 80 and 800.

Some trajectories of the number of species as a function of the number of speciations for initial connectivity 0.01 are shown in figs. 1 and 2. Antisymmetric interactions again result in large, stable systems. Symmetric interactions result in small systems. In the case of the large within-species interaction pressure (fig. 2), these have an initial shootout in size. In the case of the small within-species interaction pressure (fig. 1), the asymmetric system has repeated shootouts in size.

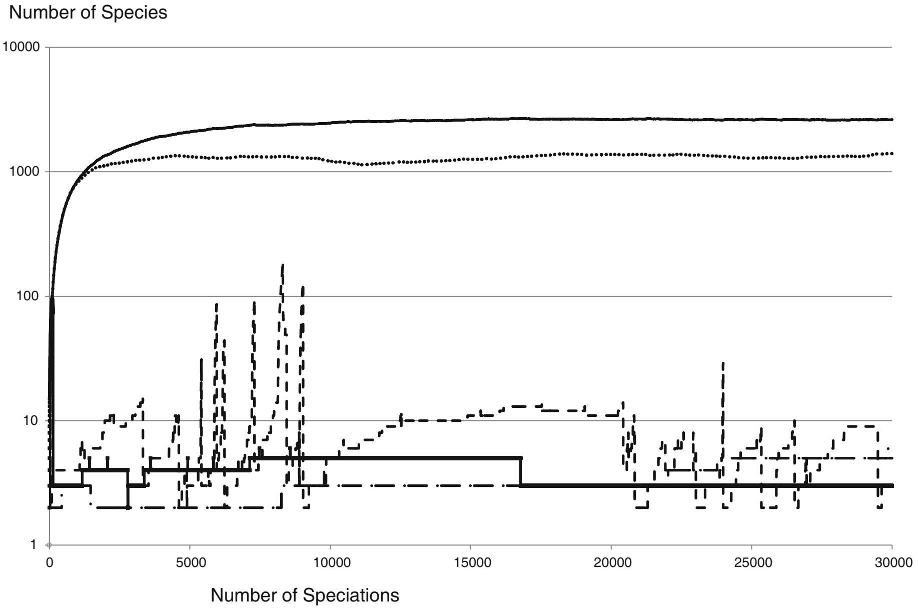

Fig. 1. Number of species as a function of speciations. Initial connectivity among species is 0.01, and within-species interaction pressure equals the standard deviation of nonzero among-species interaction coefficients. Symmetry parameter values are −1, −0.5, 0, 0.5 and 1, in the order of reducing system size.

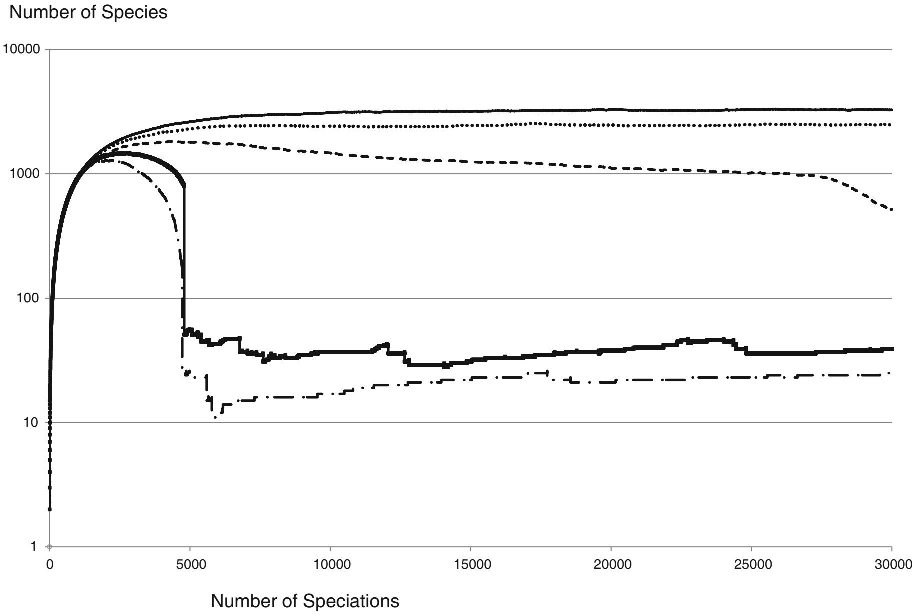

Fig. 2. Number of species as a function of speciations. Initial connectivity among species is 0.01, and within-species interaction pressure is five times the standard deviation of nonzero among-species interaction coefficients. Symmetry parameter values are −1, −0.5, 0, 0.5 and 1, in the order of reducing system size.

4 Evolution of connectivity

In the case of a fully connected system, connectivity does not evolve. This is because there is no random component in connectivity.

In the case of systems with initial connectivity 0.1, the connectivity evolved and fluctuated. The evolution and fluctuation were negligible in large, stable, antisymmetric systems. The evolution was significant in small systems, which correspond to symmetric systems. Fluctuation was most pronounced in asymmetric systems.

The evolution of system connectivity with initial value 0.01 is shown in figs. 3 and 4. We find again that in the case of large, stable systems, the connectivity does not evolve significantly (cf. figs. 1 and 2). In both figs. 3 and 4, there are two large, stable systems where connectivity remains at 0.01. Small systems with random component in the connectivity do evolve: in general, the connectivity tends to

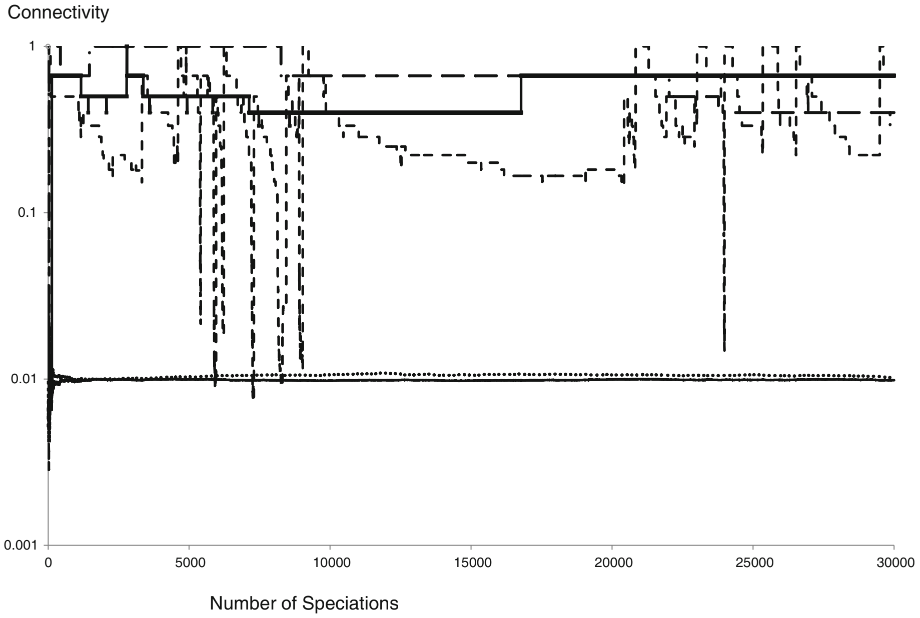

Fig. 3. Interaction matrix connectivity as a function of speciations. Initial connectivity among species is 0.01, and within-species interaction pressure equals the standard deviation of nonzero among-species interaction coefficients. The markings are the same as in fig. 1.

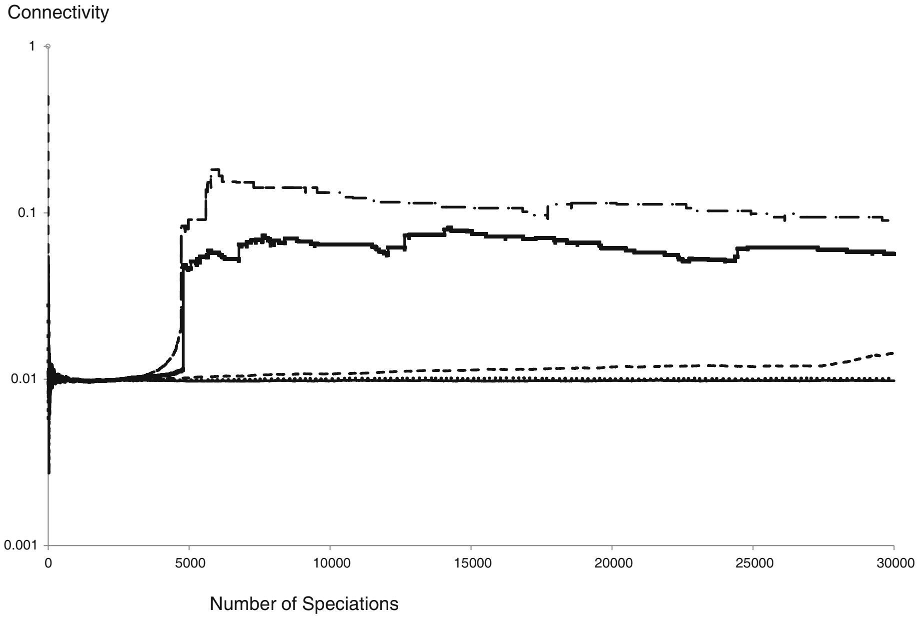

Fig. 4. Interaction matrix connectivity as a function of speciations. Initial connectivity among species is 0.01, and within-species interaction pressure is five times the standard deviation of nonzero among-species interaction coefficients. The markings are the same as in fig. 2.

increase. In both of the figures, there are two large, stable systems where connectivity is retained at 0.01, corresponding to those seen in figs. 1 and 2. There is a system in fig. 1 where species diversity fluctuates significantly, and correspondingly the connectivity fluctuates in fig. 3. A comparison of figs. 1 and 2 with figs. 3 and 4 indicates that connectivity is inversely correlated to system size: small systems are highly connected, whereas large systems remain sparsely connected. The same kind of negative correlation is visible in the case of the fluctuating asymmetric system in figs. 1 and 3.

5 Evolution of symmetry

The symmetry of any equilibrium interaction matrix between punctuations was determined by separating the antisymmetric part, determining the sum of squared matrix

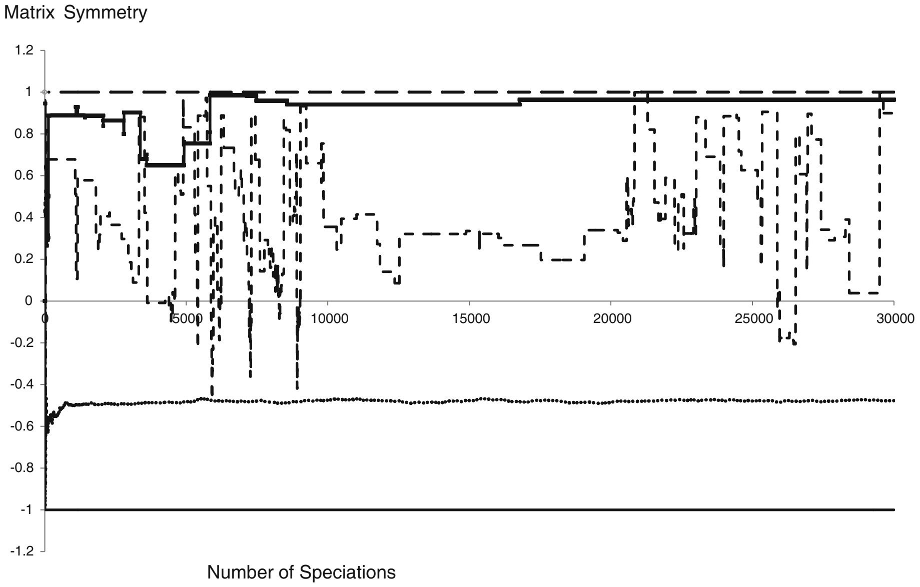

Fig. 5. Interaction matrix symmetry as a function of speciations. Initial connectivity among species is 0.01, and within-species interaction pressure equals the standard deviation of nonzero among-species interaction coefficients. The datasets are the same as in fig. 1.

elements, and relating it to sum of squared non-diagonal elements of the complete interaction matrix. This results in symmetries between zero and unity. In order to get symmetries consistent with the symmetry parameter appearing in eq. (1), the result was multiplied by −2, and then unity was added. In other words, the symmetry parameter is computed for any equilibrium interaction matrix as

$$\Gamma = -2\frac{\frac{J_{ij}-J_{ji}}{2}\frac{J_{ij}-J_{ji}}{2}}{J_{ij}J_{ij}-J_{ii}^2}+1, \tag{5}$$

where indices repeated within a term correspond to summation, and the numerator and the denominator sum separately.

In the case of a fully symmetric or antisymmetric system, the symmetry does not evolve. This is because there is no random component in symmetry. In the case of fully connected systems with small within-species interaction pressure, apart from the fully symmetric or fully antisymmetric case, symmetry did evolve. In general, the symmetry increased. In the case of the higher within-species interaction pressure, the symmetry evolved slightly but mostly fluctuated.

In the case of systems with initial connectivity 0.1, symmetries with variable components fluctuated and evolved in small, variable systems. In the case of large, stable systems that were partially antisymmetric, the symmetry did not evolve significantly.

Also in the case of systems with initial connectivity 0.01 we find that in the case of large, stable systems, the symmetry does not evolve significantly. Small systems with random component in the symmetry do evolve: in general, the symmetry tends to increase. These phenomena are demonstrated in figs. 5 and 6. In both of the figures, there are two large, stable systems, corresponding to those seen in figs. 1 and 2. In both of the figures there also is a fully symmetric system where symmetry does not evolve. Both of the figures also show two systems with evolving symmetry. In the case of fig. 5, the evolution is more pronounced, and one of the systems shows strongly fluctuating size (fig. 1), as well as fluctuating symmetry (fig. 5).

6 Evolution of average fitness

Average fitness of species within the system presumably evolves along with the extinctions of low-fitness species. From eqs. (2) and (3), the average fitness can be rewritten as

$$\overline{F} = \frac{J_{ij}x_ix_j}{\left(\sum x\right)^2}. \tag{6}$$

The number of terms in the sum in eq. (6) equals the square of the system size. However the magnitude of any term, containing a product of fractional concentrations, is proportional to system size in the power of −2. Thus, in the case of a well-connected system, the average fitness does not necessarily change with system size. On the other hand, in the case of a diagonal interaction matrix, the number of nonzero terms is linearly proportional to system size, and consequently the average fitness becomes inversely proportional to system size. Considering the fact that the diagonal of the interaction matrix predominantly contains negative elements, the average fitness would increase along with increasing system size.

According to eq. (6), the average fitness (unlike system dynamics, modulo time scale) does depend on the magnitude of interaction coefficients. We will thus normalize with the absolute predetermined mean value of the diagonal interaction matrix elements.

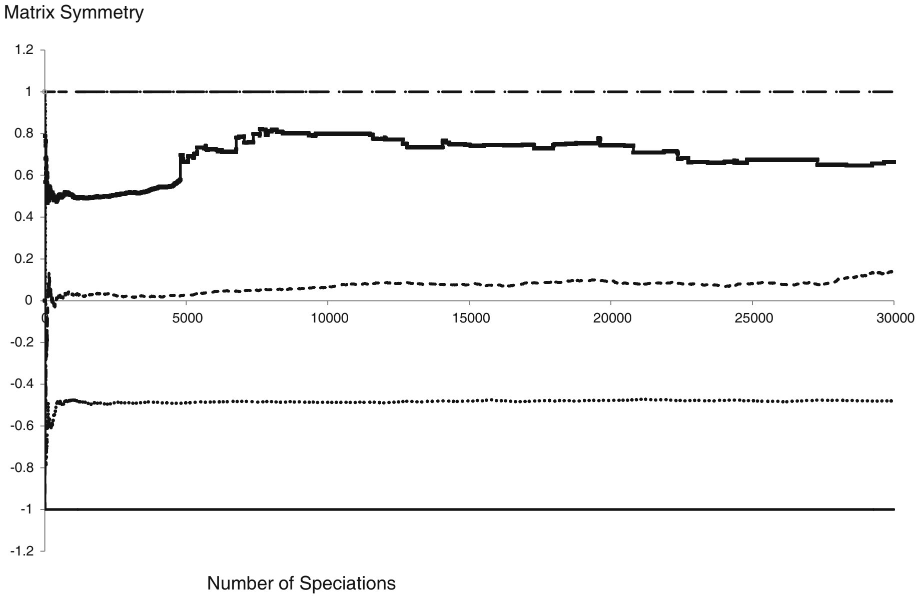

Fig. 6. Interaction matrix symmetry as a function of speciations. Initial connectivity among species is 0.01, and within-species interaction pressure is five times the standard deviation of nonzero among-species interaction coefficients. The datasets are the same as in fig. 2.

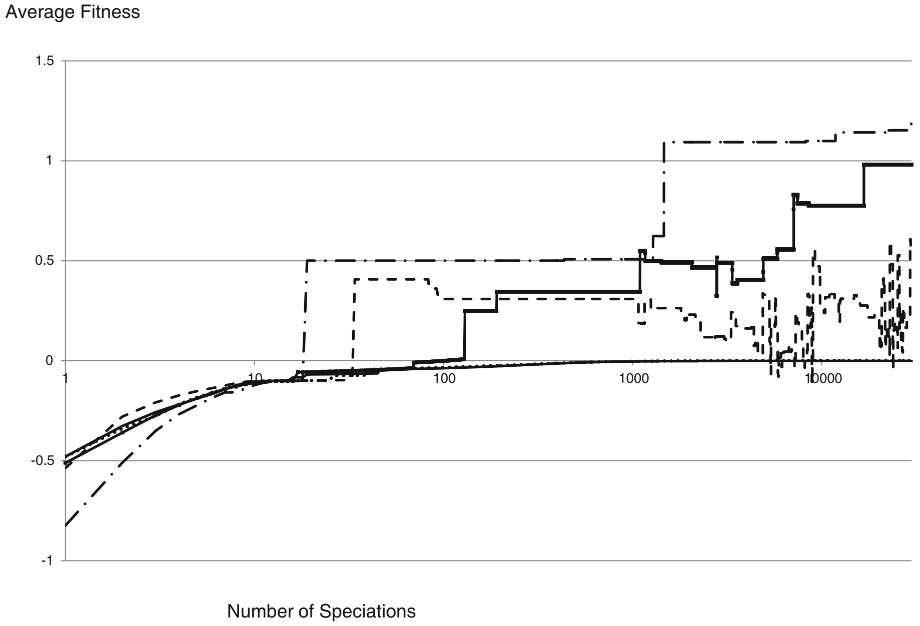

Fig. 7. Average fitness of species as a function of speciations. Initial connectivity among species is 0.01, and within-species interaction pressure equals the standard deviation of nonzero among-species interaction coefficients. The datasets are the same as in fig. 1.

We find that in the case of large, stable systems, the average fitness rapidly increases to zero and then retains this value. On the other hand, the average fitness appears to evolve continuously in small systems. In systems of fluctuating size, the average fitness appears to fluctuate. These phenomena are best demonstrated in figs. 7 and 8, which concern low-connectivity systems. In both of the figures, there are two large, stable systems, corresponding to those seen in figs. 1 and 2. The average fitness in these systems rapidly evolves to the vicinity of zero, and is then retained. I both of the figs. 7 and 8 there are three evolving systems, corresponding to figs. 1 and 2. In the case of fig. 7, the evolution is more pronounced, and one of the systems shows strongly fluctuating size (fig. 1), as well as fluctuating average fitness.

It is worth noting that in the case of a diagonal system of two species of equal concentrations and equal fitness eq. (6) results as average fitness of -0.5, and this value is

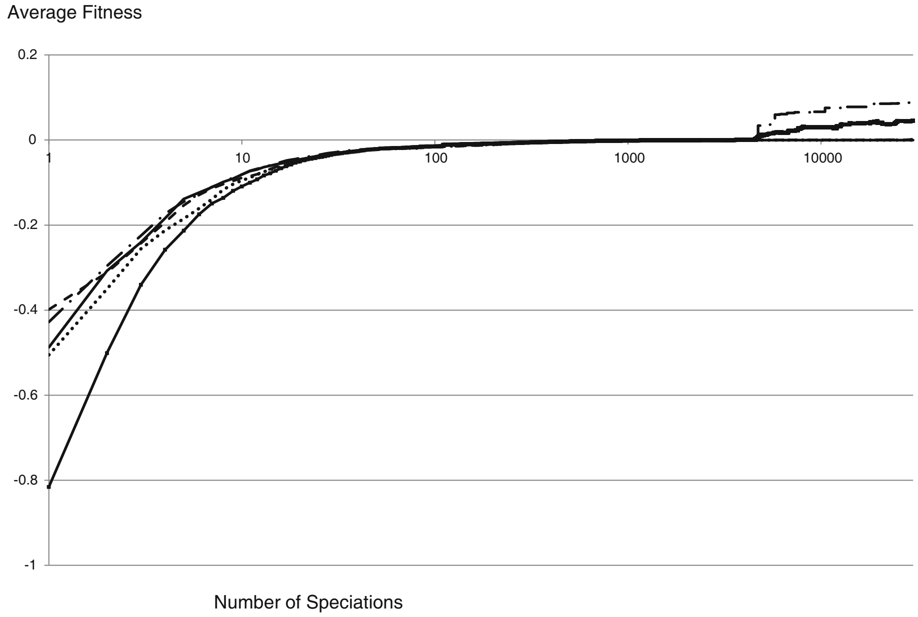

Fig. 8. Average fitness of species as a function of speciations. Initial connectivity among species is 0.01, and within-species interaction pressure is five times the standard deviation of nonzero among-species interaction coefficients. The datasets are the same as in fig. 2.

observed as a dominating initial value in figs. 7 and 8. In the case of fully connected systems (not shown in the figures), the initial average fitness is not necessary negative, and it typically evolves and fluctuates.

7 Distribution of species lifetime

Most species become extinct during their very speciation cycle, and greater lifetime probabilities are very low. However, the lifetime distribution of species varies very significantly along with the parameters. In the case of large, stable systems, some species survive over tens of thousands of speciation cycles. On the other hand, in small systems with symmetric interactions only a few of a thousand species survive until the next speciation cycle. These phenomena are demonstrated in figs. 9 and 10, which concern system of initially low connectivity. The distributions in figs. 9 and 10 have been produced on the basis of eight separate system trajectories each of 30000 speciations. In both of the figures, there are kinds of two large, stable systems, corresponding to those seen in figs. 1 and 2. In the case of fully antisymmetric systems of low connectivity, the distribution of species lifetimes is apparently skewed exponential (figs. 9 and 10). The species lifetimes certainly do not follow any power-law.

8 Distribution of number of species

The avalanche size in large, stable systems is rather narrowly distributed, almost all avalanches being smaller than ten extinct species. The number of avalanches appears to be reduced roughly in proportion to the logarithm of avalanche size. In other words, the change rate of avalanches as a function of avalanche size is approximately inversely proportional to avalanche size. The avalanche size naturally also is narrowly distributed in small systems.

Obviously, the avalanche size distribution is related to system size distribution. Large avalanches of extinction may appear only in large, variable systems. Figures 11 and 12 show the cumulative distribution of system size in relation to its maximum size. The distributions have been produced on the basis of eight separate system trajectories each of 30000 speciations. We find that significant variability appears mostly in small systems. In the case of large, stable systems, the number of living species typically is retained above 80% of the maximum. However there might be transition systems showing significant variability but also appreciable size.

Interestingly, fig. 11 shows that in asymmetric systems of moderate within-species interaction pressure over 90% of observations are confined within 10% of species abundance. This confirms that the strongly varying trajectory in fig. 1 is not coincidental. On the other hand, the distribution of species abundance in slightly symmetric systems in fig. 12 is likely to be related to the initial shootout of system size shown in fig. 2.

9 Transformation to Lotka-Volterra systems

Let us consider the mapping of the interaction matrix of the random replicator system into a generalized

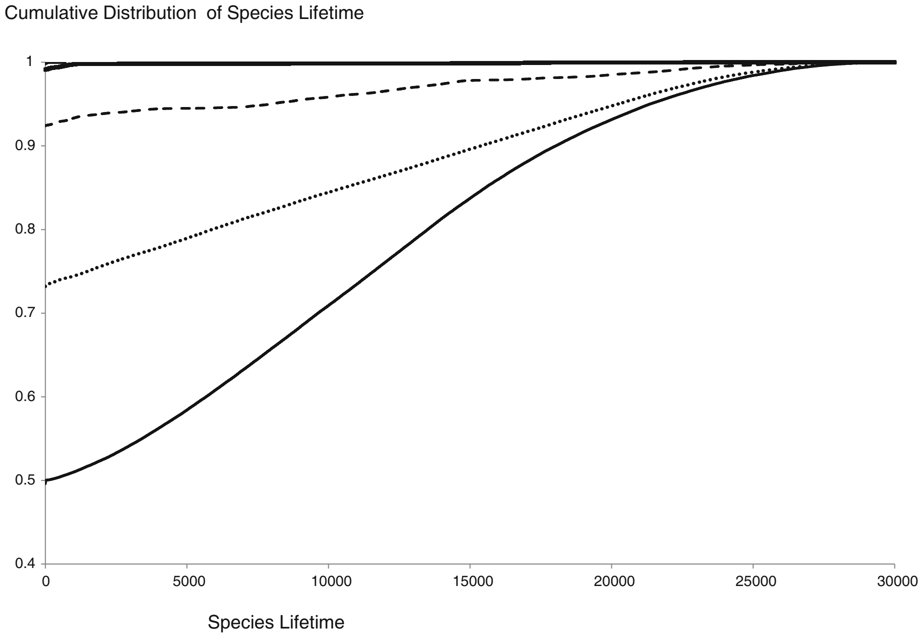

Fig. 9. Cumulative distribution of species lifetime. Initial connectivity among species is 0.01, and within-species interaction pressure equals the standard deviation of nonzero among-species interaction coefficients. The markings are the same as in fig. 1.

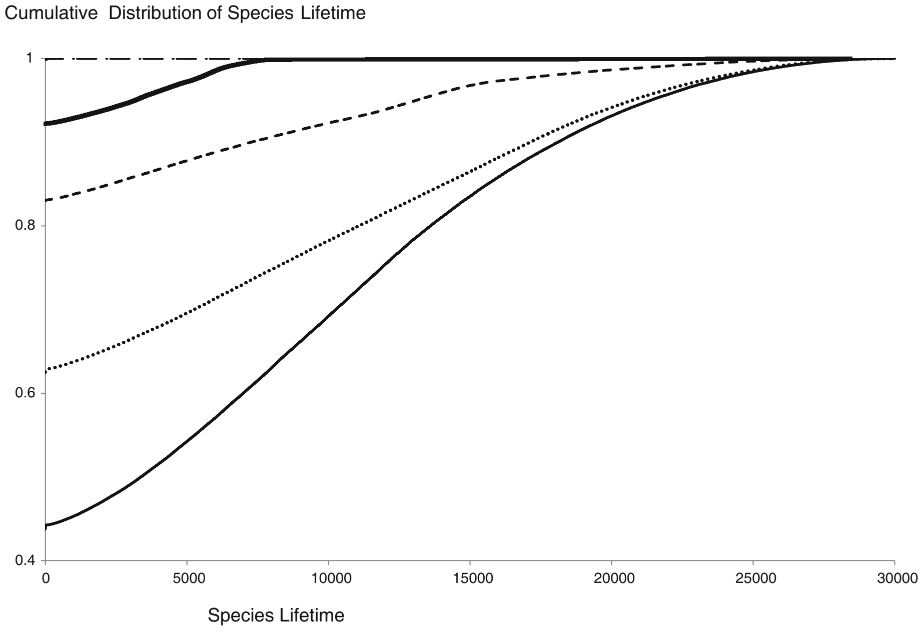

Fig. 10. Cumulative distribution of species lifetime. Initial connectivity among species is 0.01, and within-species interaction pressure is five times the standard deviation of nonzero among-species interaction coefficients. The markings are the same as in fig. 2.

Lotka-Volterra system [33] as

$$A_{ij} = J_{ij} - \frac{J_{ij} x_i}{\sum x}\,, \tag{7}$$

where A_{ij} are the Lotka-Volterra interaction coefficients, giving the effect of species j concentration on the relative change rate of species i concentration.

It is worth noting that several properties of the interaction matrix may change along with the mapping. Firstly, vacancies vanish from the interaction matrix. The Lotka-Volterra system corresponding to an arbitrary replicator system is in general almost fully connected, even if some of the connections may be weak. Secondly, symmetries may change. Thirdly, the relative contribution of among-species interaction may change.

We find that from fig. 13 that the symmetry of a Lotka-Volterra system, determined according to eq. (5), does not differ drastically from the corresponding replicator

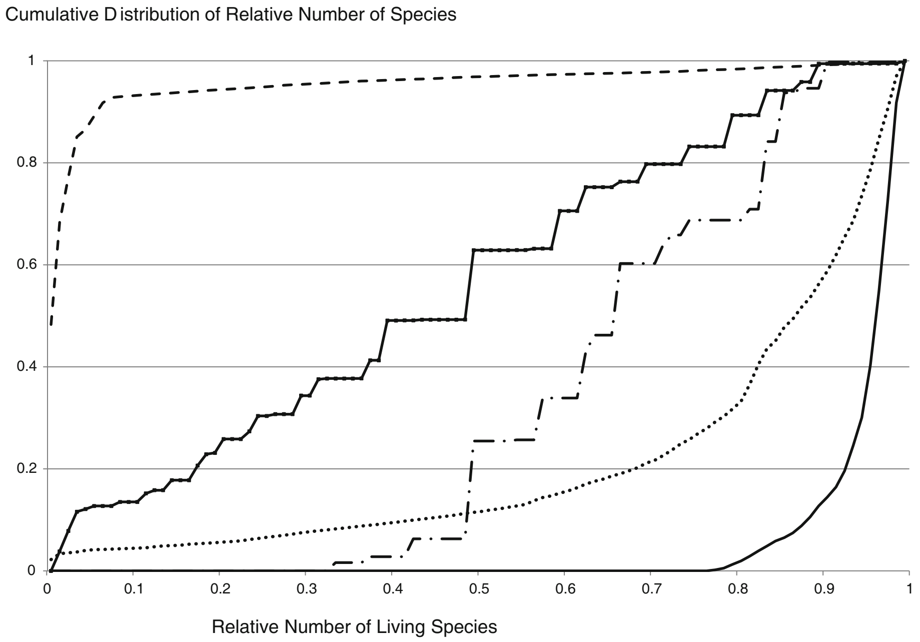

Fig. 11. Cumulative distribution of relative number of species. Initial connectivity among species is 0.01, and within-species interaction pressure equals the standard deviation of nonzero among-species interaction coefficients. The markings are the same as in fig. 1. The first 5000 speciation cycles are excluded from the data.

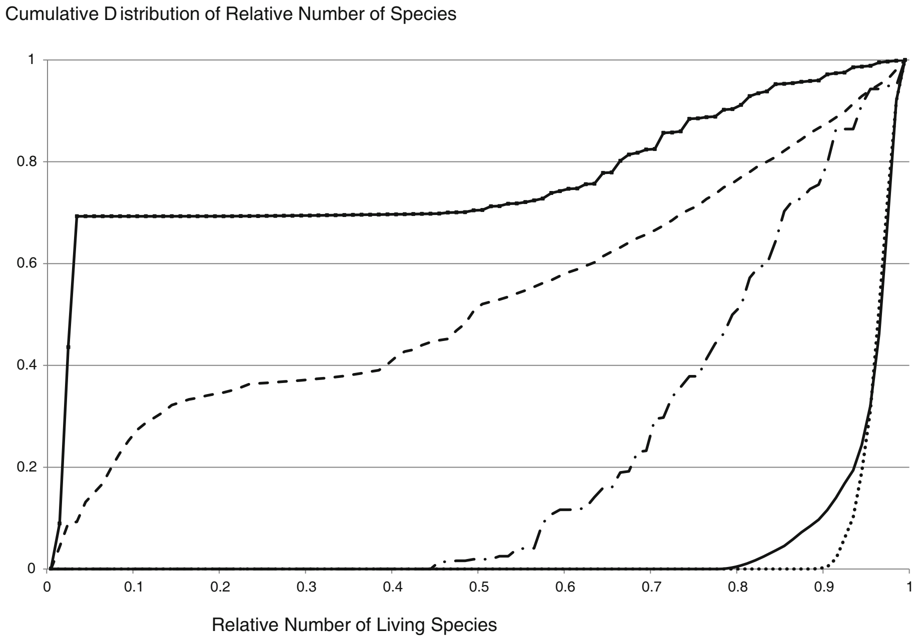

Fig. 12. Cumulative distribution of relative number of species. Initial connectivity among species is 0.01, and within-species interaction pressure is five times the standard deviation of nonzero among-species interaction coefficients. The markings are the same as in fig. 2. The first 5000 speciation cycles are excluded from the data.

system. In cases where the symmetry of a replicator system evolves significantly, also the symmetry of the corresponding Lotka-Volterra system evolves (fig. 13, cf. fig. 5). The same is true for the larger within-species interaction pressure (cf. fig. 6), as well as for initial connectivity 0.1.

The relative magnitude of among-species interaction is defined as the sum of squared among-species interaction coefficients in relation to the sum of squared within-species interaction coefficients. In other words, the relative magnitude of among-species interaction is

$$ASI = \frac{J_{ij}J_{ij} - J_{ii}^2}{J_{ii}^2} \tag{8}$$

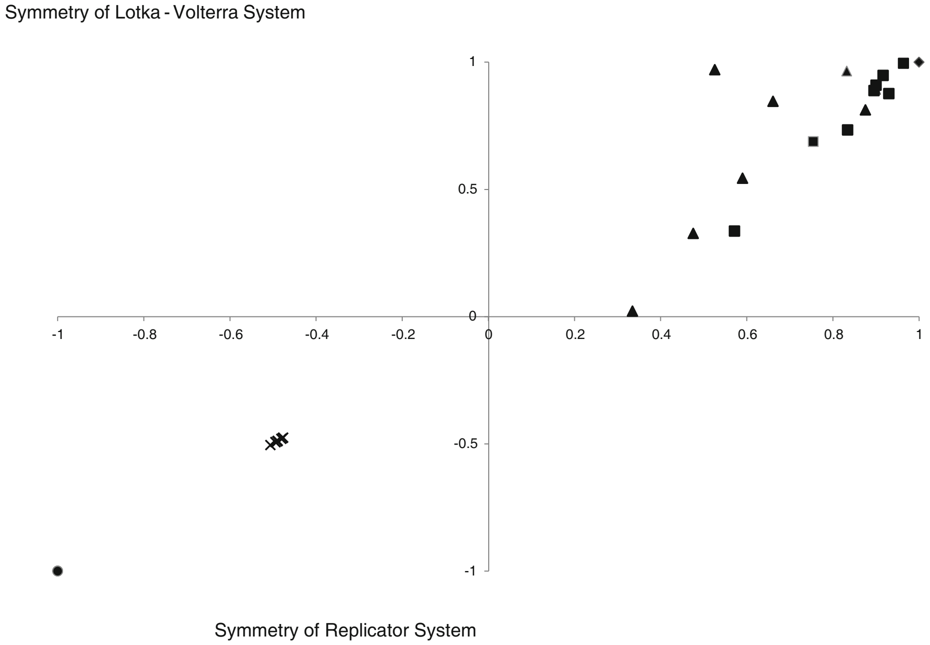

Fig. 13. Interaction matrix symmetry within a Lotka-Volterra system, as a function of the symmetry of the replicator system. Initial connectivity among species is 0.01, and within-species interaction pressure equals the standard deviation of nonzero among-species interaction coefficients. Symmetry parameter values are -1 (circles), -0.5 (crosses), 0 (triangles), 0.5 (squares) and 1 (diamonds). Mapping of the replicator system into the Lotka-Volterra system has been after 5000 and 30000 cycles of speciation.

and similarly for the Lotka-Volterra coefficients A_{ij}. Again, the numerator and the denominator sum separately.

We find that from fig. 14 that the relative among-species contribution within a Lotka-Volterra system may differ drastically from the corresponding replicator system. In particular, in small systems with relatively weak within-species interaction and consequently relatively strong among-species interaction, the Lotka-Volterra system tends to show significantly lower relative among-species interaction (fig. 14).

10 Discussion

The evolution of a system of species in terms of random replicator networks was investigated. The mathematical model results in finite size of ecosystems as reported in figs. 1 and 2. The absolute ecosystem size naturally depends on model parameters. The average species concentration in relation to the speciation concentration is

$$\frac{\overline{x}}{\varepsilon} = 1 + \frac{1}{n\varepsilon}\,, \tag{9}$$

where n is the number of species. eq. (9) simply results from the first species appearing at unit concentration, and the following species at concentration ε. Equation (9) indicates that the ecosystem size depends on the choice of the speciation concentration.

The replicator ecosystems investigated in this paper become large and complex, provided the interactions are predominantly antisymmetric. This corresponds to systems with predators and parasites, instead of systems consisting of mutually competitive or symbiotic species. A co-dominating feature is within-species interaction pressure: large within-species interaction increases species diversity. Even if species diversity is the larger the greater the within-species interaction pressure and the lower the connectivity, both of these factors reduce the relative contribution of among-species interaction on species fitness.

Average fitness evolves in all systems, however symmetry and connectivity evolve in small systems only. Newcomers get extinct almost immediately in symmetric systems. Even in antisymmetric systems, they have the greatest extinction probability, the distribution in species lifetimes being apparently skewed exponential. Thus most of the species have a short lifetime, whereas some endure. This appears to correspond with paleontological findings [47,42,48,49].

The size of extinction avalanches being narrowly distributed, the replicator ecosystems appear either large and stable or small and possibly variable. Fluctuations of all magnitudes, probably distributed according to a power-law, might imply criticality [5]. Consequently the replicator ecosystems do not appear as critical systems. Transition systems between small, variable and large, stable systems can be produced by tuning the parameters. Such systems may have a significant magnitude of variation. However there is no indication that the replicator ecosystems would self-organize into a critical state. Provided the evolution of a system of species in Nature is a self-organized critical process [1–5], the replicator ecosystems investi-

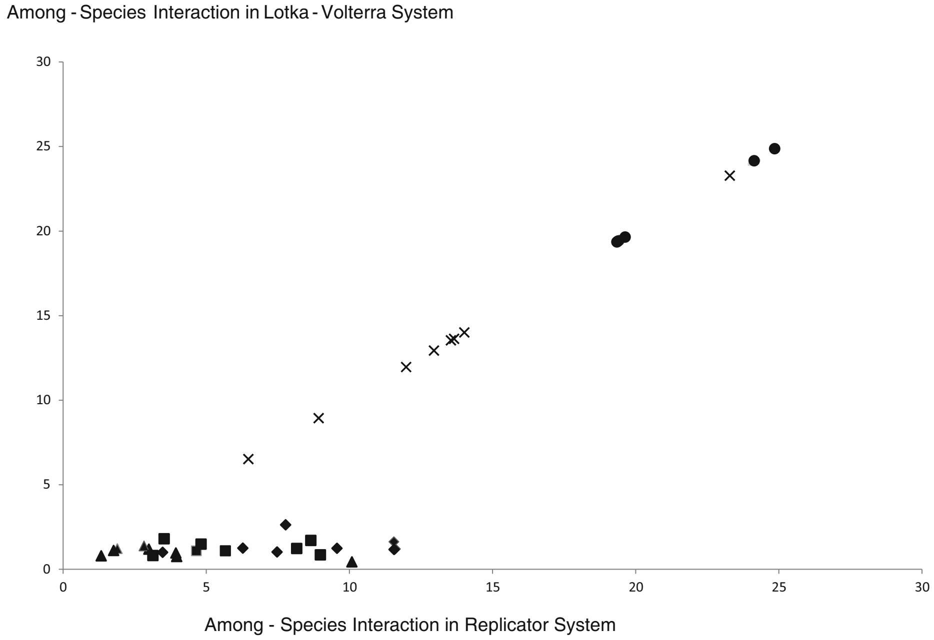

Fig. 14. Relative magnitude of among-species interaction within a Lotka-Volterra system, as a function of the among-species interaction within the replicator system. Initial connectivity among species is 0.01, and within-species interaction pressure equals the standard deviation of nonzero among-species interaction coefficients. Symmetry parameter values are -1 (circles), -0.5 (crosses), 0 (triangles), 0.5 (squares) and 1 (diamonds). Mapping of the replicator system into the Lotka-Volterra system has been after 5000 and 30000 cycles of speciation.

gated in this paper do not appear to reproduce this feature. Such a feature however is not indisputable [42,4,24].

It is worth noting that changing nearest-neighbor interactions into random interactions, deteriorating spatial power-law correlations into a delta function, appear to deteriorate self-organized criticality in a classical toy model of evolution, even if some power-law distributed observables remain [44]. However, even systems without spatial correlations may be considered critical provided activity does not vanish, but infinitely retains the fractal temporal geometry [44,39].

It certainly would be of academic interest to introduce one-dimensional nearest-neighbor interactions into the replicator system. Two-dimensional spatial interactions certainly would have more correspondence with real life. Such an arrangement might partially correspond to metapopulation dynamics [50–54]. Clarification of spatial correlations in replicator system however might be computationally rather demanding.

Transition to generalized Lotka-Volterra system does not significantly affect symmetry or relative dominance of within-species interaction in large, complex systems. In small, variable systems, the relative dominance of within-species interaction appears greater in the Lotka-Volterra interaction matrix.

Regarding the Lotka-Volterra system, any differential change of species concentration is the same as in the case of the replicator system (eq. (3)), provided the interaction matrix is as given in eq. (7). However the interaction matrix given in eq. (7) depends on the species concentration vector, in addition to the interaction matrix of the replicator system. This means the interaction matrix should be reproduced every time the concentrations change. Finding an equilibrium species concentration after any speciation event typically requires many changes in the species concentration vector. In this sense, the Lotka-Volterra model may be viewed as a tedious way of implementing the random replicator model.

It is still worth considering why the symmetry of the corresponding Lotka-Volterra system does not differ drastically from the symmetry of the replicator system. The latter term of eq. (7) actually is a column-differential of the average Fitness (eq. (6)). In the case of large systems, the latter term of eq. (7) may average towards zero. This obviously is the case if the average fitness develops towards zero (cf. eq. (6), figs. 7 and 8). In the case of small systems, an eventual reason may be that the latter term of eq. (7) tends to have symmetries which do not drastically differ from the symmetries of the first term. The latter may hold in particular if the small systems are symmetric, as they tend to be in the present results (fig. 5).

Another issue worth considering is why the relative among-species contribution of the corresponding Lotka-Volterra system mostly does not differ from that of the replicator system, but does become reduced in small systems with weak within-species interaction (fig. 14). In the case of large, stable systems, where the latter term of eq. (7) sums towards zero (eq. (6), fig. 5), there actually is not much difference in the interaction matrices of the Lotka-Volterra and the replicator systems. In the case of small, variable systems the average fitness is predominantly positive (fig. 7). Then, the latter term in eq. (7)

is predominantly positive. Consequently, the magnitude of the diagonal terms is increased by eq. (7), which reduces the relative magnitude of among-species interaction within the Lotka-Volterra interaction matrix. It is however still worth noting that, the Lotka-Volterra model possibly is not much more than a tedious way of implementing the random replicator model.

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