The Evolution of Diversity in Replicator Networks

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Abstract

Novel species are introduced into a network of interacting replicators either (i) as mutants of members of the network or (ii) as unrelated immigrants. We consider the meta-population dynamics of such a system. In the first case the appearance of mutants leads to a slow growth of the replicator network, proportional to the logarithm of the number of mutation events. Surprisingly, replicator evolved by mutant incorporation are always permanent, despite the fact that permanence is in general a very rare phenomenon. In the second case, on the other hands, immigrants lead to frequent break-downs of the entire network and hence to complete extinction. In both cases individual species are short-lived, the distribution of survival times is exponential.

Keywords

Replicator Equation — Meta-population Dynamics — Mutation — Immigration — Permanence

1. Introduction

Self-replication on molecular level is the crucial "invention" for the origin and maintainance of life. One of the central questions in any theory of molecular evolution concerns the evolution of a collection of competing (or otherwise interacting) species of replicators $I_1, \ldots, I_n$. There is a well developed theory for the most simple reaction scheme

$$I + E \rightarrow 2I + E\,, \qquad (Q)$$

namely the theory of the *molecular quasi-species* (Eigen, 1971; Eigen *et al.*, 1988; McCaskill, 1984). Here the enzyme (protein) E is part of the environment provided by the experimentalist. This framework has been very successful in describing the evolution of RNA viruses (Eigen *et al.*, 1988).

Nowadays, most experts agree that RNA, or an RNA-like precursor, was the first replicator in the history of life (Eigen *et al.*, 1981; White, 1976). In fact, the discovery of catalytically active RNAs (Cech, 1986; Cech, 1988; Guerrier-Takada & Altman, 1984; Westheimer, 1986) and in particular the discovery of ribozymes with RNA-replicase-like properties (Been & Cech, 1988; Ekland & Szostak, 1996; Hager *et al.*, 1996) make this assumption very persuasive. In its most condensed form the logics of an RNA world is captured in the *autocatalytic reaction network*

$$I_k + I_l \;\longrightarrow\; 2I_k + I_l \qquad\qquad k,l = 1,\ldots,n. \qquad (A)$$

A wealth of knowledge on this model has accumulated over the last two decades beginning with a theory of the hyper-cycle model (Eigen & Schuster, 1977; Eigen & Schuster, 1978a; Eigen & Schuster, 1979). The associated dynamical system is the *second order replicator equation* (Schuster & Sigmund, 1983)

$$\dot{x}_k = x_k \left(\sum_{j=1}^{n} a_{kj} x_j - \sum_{i,j} a_{ij} x_i x_j \right) . \tag{1}$$

It is based on the chemical reaction scheme (A) and the assumption of *constant organization*, that is, the conservation of the total amount of replicators. The variables x_k are relative concentrations of replicating the species I_k. Originally developed as a model of prebiotic evolution replicator equations have been encountered since then in many different fields: populations genetics, mathematical ecology (where they occur disguised as Lotka-Volterra equations (Hofbauer, 1981)), economics, or laser physics. Their properties have been the subject of hundreds of research papers by many research groups. The results of the first decade of investigation are compiled in the book (Hofbauer & Sigmund, 1988). Although successful attempts have been made to include mutation, see for example (Biebricher *et al.*, 1991; Stadler & Schuster, 1992; Happel & Stadler, 1996), no *new* species are introduced externally in these models, which consider the population dynamics of a fixed replicator network with sloppy replication rather than the evolution of replicator networks.

In this contribution we adopt a different point of view. Instead of concentrating on the population dynamics of a replicator network we shall study its reaction to the introduction of a new species. While this "opens" our model allowing for a variable number of species, we still enforce the "constant organization" constraint at the level of concentrations. In technical terms, we change the dimensionality of the matrix $\mathbf{A}$ in equ.(1) while retaining the form of the replicator equation. Our main focus will be the evolution of diversity in such replicator networks, in particular, the evolution of the number of species.

The catalytic hyper-cycle (Eigen & Schuster, 1977; Eigen & Schuster, 1978a; Eigen & Schuster, 1978b) was introduced as a possibility to overcome the restrictions on the amount of genetic information that can be inherited by non-autocatalytic replication schemes (Eigen, 1971). Soon it was discovered, however, that hyper-cycles are vulnerable to parasites. In addition, the fraction of replicator networks that is hyper-cycle-like in the sense that it guarantees the permanent coexistence of all its members (in a population dynamics sense) decreases exponentially with the number n of coexisting species (Stadler & Happel, 1993). Even though large networks are rare, they might still be an (almost) unavoidable outcome of evolution.

May and Nowak (May & Nowak, 1994) analyzed the evolution of a simple Lotka-Volterra type model of super-infection in host-parasite associations (Nowak & May, 1994). Interestingly, the same type of equations was obtained by Tilman (Tilman, 1994) in a study on *competition and biodiversity in spatially structured habitats*. The total number of species in their system slowly increases, $n(\tau) \sim c \ln \tau$, where τ is the number of mutation events. Their super-infection model, however, models parasite species by only two parameters: virulence and transmission efficiency, while the host is merely viewed as a substrate and does not evolve at all. More recently May and Nowak (May & Nowak, 1995) found a square root law $n(\tau) \sim \sqrt{\tau}$ in coinfection model that neglects competition of different parasites within the same host. It is by no means clear that a less restricted types of replicator network will show a similar increase of diversity. In this contribution we simulate the meta-population dynamics of autocatalytic networks using two extremal mechanisms: (i) *mutation* of one of the members of the network and (ii) *immigration* of a completely unrelated species.

The first case leads to slow growth of the number of species, and surprisingly to the selection of permanent networks. Immigration, on the other hand leads to frequent catastrophic extinction events that preclude a long term growth of the number of surviving species. The long-time behavior of the meta-population dynamics thus depends crucially on the mechanism by which new species are introduced into the system.

2. The Evolution of Replicator Networks

2.1. Mutants and Immigrants

We start with a 2-species network with randomly chosen interaction matrix $\mathbf{A}$. (A 1-species replicator equation is trivial, since $x_1 = 1$ and $\dot{x}_1 = 0$. Without loosing generality we may assume that the diagonal entries of $\mathbf{A}$ are zero since the addition of a constant to each column does not affect the dynamics (Hofbauer & Sigmund, 1988). The replicator equation is integrated[1] until the trajectory has reached its ω-limit. A novel species is introduced into the existing network by extending $\mathbf{A}$ with an extra row r and an extra column c:

$$\mathbf{A} \longrightarrow \begin{pmatrix} \mathbf{A} & c \\ r & 0 \end{pmatrix} . \tag{2}$$

The coefficients collected in r and c describe how the new member interacts with the existing species. The extended interaction matrix is again in "normal form", i.e., all diagonal elements of the matrix $\mathbf{A}$ are 0. The next step is a perturbation in the concentrations of the existing species. We set $x_k \to x_k - \delta/n$ and $x_{n+1} = \delta$. Again we integrate the differential equation until the trajectory $x(t)$ has reached its ω-limit[2]. If the concentration x_k of a species becomes 0, i.e., if it falls below a very small threshold, the corresponding row and column is removed from the interaction matrix.

This scheme assumes that the time intervals between mutations or immigration events are much longer than the time scale of the population dynamics itself. Numerical experiments suggest that if the time between two perturbations of the dynamical system is not long enough to reach equilibrium, then the number of species will rapidly grow, since the time for extinction is not sufficient before the next new species appears. The number of species will increase almost linearly for some time until the system collapses and only a very small number of species

[1] All programs were written in `C`. Several subroutines from the public-domain libraries `ODEpack`, `LAPACK` and `LINPACK` were used.

[2] The $\omega - limit$ of a trajectory with initial condition $x(0)$ is the set of its accumulation points. It depends on the initial conditions and describes the long time behavior of the dynamics. The ω-limit of a trajectory is in most cases a fixed point, a periodic limit cycle, a strange attractor, or a heteroclinic cycle.

survives. Then the process repeats. The long term behavior of the model is determined in this case by the after-collapse networks. They seem to conform the rare perturbation scenario, hence only the latter was investigated in detail.

The properties of the newly introduced species are determined by the vectors r and c. We may distinguish immigrants and mutants:

- An *immigrant* is a species that has random interactions with all species in the existing network. Hence we randomly generate a row r and a column c to the interaction matrix $\mathbf{A}$. A parameter ϵ determines the size of the entries relative to the entries in $\mathbf{A}$.
- A *mutant* is obtained by randomly choosing a species from the network and by modifying it in such a way that the novel species interacts in a similar way with the rest of the network.
  More precisely, we choose $r_i = a_{pi} + \epsilon_i$ and $s_j = a_{jp} + \epsilon_j$ where the ϵ's are independent, identically distributed (i.i.d.) random variables with mean 0. The elements of $\mathbf{A}$ are "inherited" from the previous iteration. We shall see below that the survival times of individual species are short, hence the initial conditions are soon wiped out in a simulation run.

2.2. The Probability of Invasion

Replicator equations "live" on a simplex S_n. A face of this simplex characterized by the set K of extinct species, i.e., $k \in K$ if and only if $x_k = 0$. We shall sometimes write x^K in order to emphasize that x lies in the interior of k-face. An eigenvalue of the Jacobian of a fixed point $\hat{x}^K$ is *transversal* if the corresponding eigenvector points into the interior of S_n. For second order replicator equations these eigenvalues can be computed explicitly (Hofbauer, 1986):

$$\lambda_k(\hat{x}^K) = [\mathbf{A}\hat{x}^K]_k - (\hat{x}^K \mathbf{A}\hat{x}^K) \qquad \text{if} \quad k \in K \tag{3}$$

The new species can invade the existing network at least temporarily if its concentration $x_{n+1}(t)$ grows, that is, if $\dot{x}_{n+1}(0) > 0$, where 0 denotes the time of the mutation or immigration event. This condition is satisfied if and only if the transversal eigenvalue $\lambda_{n+1}(x)$ is positive. If the network was in an equilibrium before the invasion, then x is the interior rest point $\hat{x}$ of this network. Otherwise x is a point in an ω-limit that is contained in the interior of the simplex S_n. The time

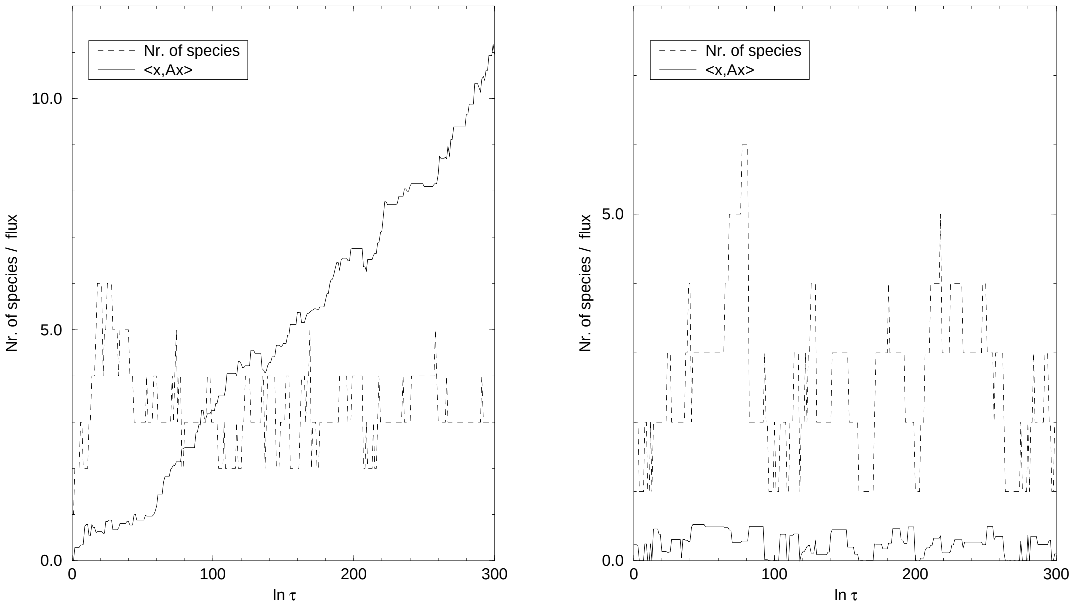

Figure 1: Evolution of the mean fitness (flux) Φ.
(a) The average fitness increases with repeated mutations. Note the this increase is a strong trend but it is not strictly monotonous.
(b) The average fitness does not increase in the immigration model due to frequent breakdowns of the system, in which all but one species disappear. The mean fitness is reset to $\Phi = 0$ at such catastrophic events.

average of any trajectory within such an ω-limit is again the interior equilibrium $\hat{x}$ (Hofbauer & Sigmund, 1988). We may therefore use $\lambda_{n+1}(\hat{x})$, where $\hat{x}$ is the interior rest point of the old network.

Theorem. If a new species is introduced by mutation into an equilibrated second order replicator network, the probability of invasion is independent of the of the old species.

Proof. For the relevant transversal eigenvalue we have

$$\begin{aligned}\lambda_{n+1} &= (\mathbf{A}\hat{x})_{n+1} - \langle \hat{x}, \mathbf{A}\hat{x} \rangle \\ &= \sum_{j=1}^{n} \epsilon_j \hat{x}_j + \underbrace{\sum_{j=1}^{n} a_{kj}\hat{x}_j - \sum_{l,m=1}^{n} a_{lm}\hat{x}_l\hat{x}_m}_{=0} = \sum_{j=1}^{n} \epsilon_j \hat{x}_j \,.\end{aligned}$$

The second term vanishes since $\hat{x}$ is an equilibrium. Since the ϵ_j are i.i.d. with

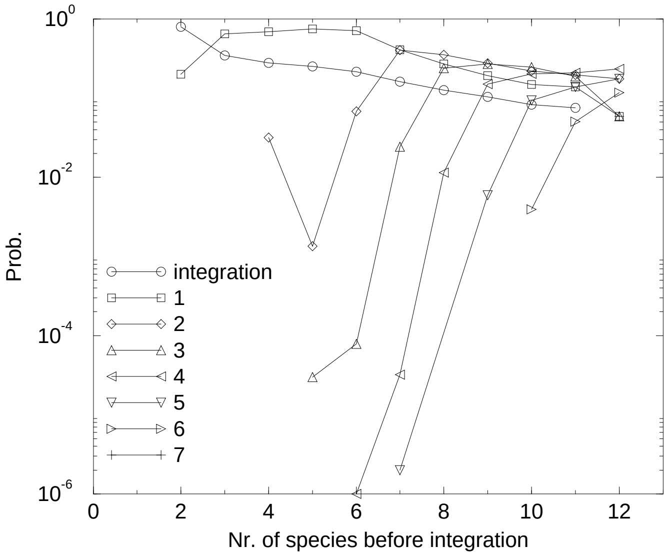

Figure 2: Mutation model: The probability that a species invading a network of n species kills a certain number of old ones. Different numbers of extinct species are indicated by different symbols. An open circle, $\circ$, denotes the fraction of mutation events that enlarge the network.

mean 0, the expected value of $\lambda_{n+1}(\hat{x}) = 0$ and thus $\lambda_{n+1}(\hat{x}) > 0$ with probability 0.5 independent of $\mathbf{A}$. ∎

The distribution of ϵ_j's in mutants that are eventually incorporated into the network will therefore be biased to have a positive expectation value. Thus the equilibrium flux $\Phi = \sum_{ij} a_{ij}\hat{x}_i\hat{x}_j$ should on average increase with time. Figure 2a shows that this is indeed the case.

In the case of immigration the situation is different. Since r and c are now completely unrelated to the entries in the old interaction matrix we find

$$\lambda_{n+1} = \sum_{j}^{n} r_j\hat{x}_j - \sum_{l,m}^{n} a_{lm}\hat{x}_l\hat{x}_m = \sum_{j}^{n} \hat{x}_j(r_j - a_{kj}) \tag{4}$$

for some $k \leq n$. Here we used $(\mathbf{A}\hat{x})_k = (\hat{x}\mathbf{A}\hat{x})$. The probability of invasion will therefore depend on the structure of the existing network.

Invasion is only a short-time effect. We are more interested in the long-time effects mutant or immigrant intrusion. What is the effect of an invader, be it a mutant or an immigrant? Three scenarios are possible: The intruder is incorporated into the network (which then grows from size n to size $n+1$), it may be expelled from the system after some time, or it may causes the extinction of one or more of the previously coexisting species. All three scenarios occur with both mutants and immigrants, although with vastly different probabilities.

The probability distributions of different types of the size-changes of the evolving networks are summarized in figure 2 for mutation. The probability of integration of a mutant and the probability of replacement of a single species decrease slowly with the size of the system. Large changes in the size of the system, however, become much more likely with increasing network size. Indeed the most likely changes reduce the number of species to the average value of 5 or 6 survivors. The situation is very different in the immigration case: a substantial fraction of immigrants wipes out the entire network, see figure 1.

2.3. The Evolution of Diversity

In the immigration model we repeatedly encounter catastrophic events that wipe out the entire network. The number of interacting species fluctuates between 1 and 4 most of the time. The average value soon settles down at about 2.72. Since a reduction $n(\tau)$ to 1 is equivalent to a restarting the entire simulation there is no slow growth of the expected number of species with τ, see also figure 1b.

In the mutation case we observe a transient phase of a few thousand events in which the average number of species increases to an average of about 5 to 6. A close inspection shows that after the first 10^5 mutation events the average number of species increases by about 0.22 during the next 10^6 cycles. The logarithmic plot in figure 3 shows that the data are consistent with a logarithmic increase in the number of species. We find $n(t) \sim 0.065 \ln \tau$. This results parallels the result in (May & Nowak, 1994) for the super-infection model, except that the slope is much smaller in the case of general replicator equations.

We conclude that an increase in diversity is a generic feature of evolving replicator networks, not a property of a particular network organization. On the other hand, it depends crucial on the correlation between pre-existing species and intruder: only mutants of established network members lead to long-term growth, while unrelated immigrant species will eventually kill the replicator network.

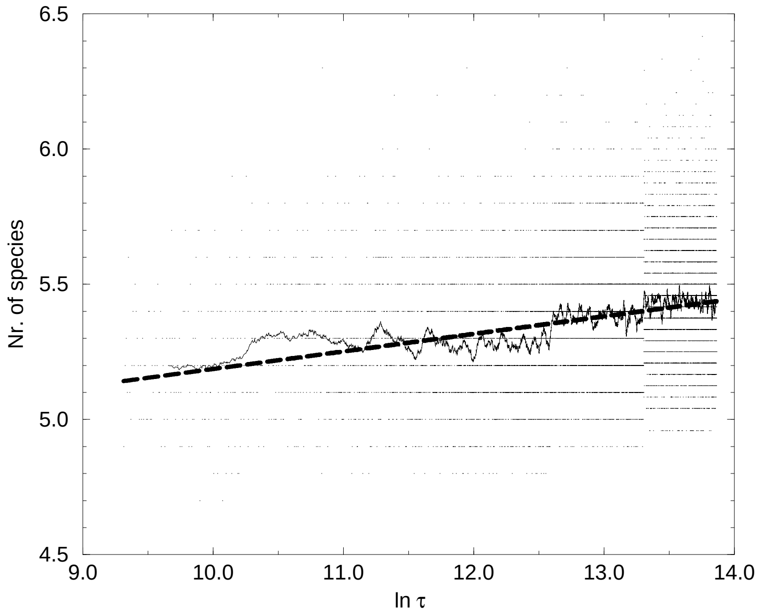

Figure 3: Evolution of diversity by mutation. The graph shows the average number of species after τ events averaged over 10 to 20 independent simulations. The full line is a running average (window size 100 events), the dashed line is least square fit. The data are consistent with $n(\tau) \sim 0.065 \ln \tau$.

The distribution of the number of living species settles down to an approximately stationary distribution in the mutation model, except for the very slow increase of the mean discussed above. The l.h.s. of figure 4 shows the distribution of network sizes (after the transient period). It is independent of the size of the mutations. In the immigration case we observe a significant dependence on the average strength ϵ of the interactions of the immigrating species relative to the average strength of the interactions within the invaded network. We find an increased number of large networks (with up to 9 species) for $\epsilon < 1$, see the r.h.s. of figure 4. The average number of species does not strongly depend on ϵ, however.

2.4. The Evolution of Permanence

Few dynamical systems allow a complete analytical treatment. In any event, one often is not interested in all details of a dynamical system or in the structure of its ω-limit sets, so that less detailed knowledge may well be sufficient. In the context of this study the most important question is: *Can all species coexist in the system*

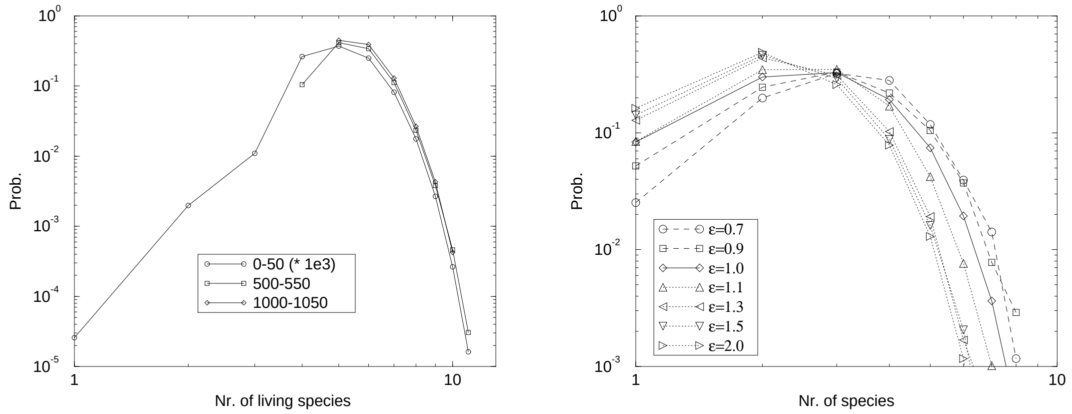

Figure 4: The Probability to find a given number of living species after a randomly chosen cycle.
l.h.s.: Mutation case. Small networks with less than 3 species appear only in the initial phase of a simulation. After about 50000 cycle the distribution does not change significantly (the rightmost curve show the distribution after 10^6 cycles).
r.h.s.: Immigration case. The probability depends on the size of the entries in the row r. A value of $\epsilon = 1$ means that the interactions of the new species with the old network are of the same strength as the average interaction within the old network. We show distributions for $0.7 < \epsilon < 2.0$.

for arbitrarily long time, or will some species die out in the long run? Schuster *et al.* (1979) introduced the notion of *permanence*, or permanent coexistence, to formalize this question. A variety of related notions of cooperation, the first of which is now called *weak persistence* (Freedman & Waltman, 1977), have been proposed by various authors. For an overview see (Freedman & Moson, 1990; Hutson & Schmitt, 1992).

By construction, all species survive for infinitely long time in "equilibrated" replicator networks. Permanence, however, is a much stronger concept. It implies that the boundary of the simplex S_n is a repellor, that is, survival is guaranteed under small perturbations and independent of initial conditions. Formally, permanence is defined as follows, see e.g., (Schuster *et al.*, 1979; Hofbauer & Sigmund, 1987): Let S be a closed subset of $\mathbb{R}^n$ and let $f : S \to \mathbb{R}^n$ be such that the solutions $x(t) \in S$ of the initial value problem $\dot{x} = f(x)$, $x(0) = x_0$ is unique and defined for all $t \geq 0$. This dynamical system is called *permanent*, if all orbits are uniformly bounded and there is a compact set C entirely contained in the interior of S, such that for all $x \in \operatorname{int} S$ holds $\omega(x) \in C$.

In general it is not easy to check whether a given dynamical system is permanent. So far, there is only one necessary and sufficient condition for permanence, namely the existence of a so-called *average Lyapunov function* (Hofbauer, 1991; Hutson, 1984; Hutson, 1988). As a consequence of Brower's fixed point theorem permanence implies the existence of an equilibrium point in the interior of S (Hutson & Vickers, 1983). A rest point $\hat{x}^K$ is called *saturated* (Hofbauer, 1986) if all its transversal eigenvalues are non-positive. A permanent catalytic network has no saturated equilibria at the boundary. Jansen (Jansen, 1986) showed that a second order replicator equation is permanent if there is a vector $p \in \operatorname{int} S_n$ such that for all isolated rest points $\hat{x}^K$ on the boundary of S_n holds

$$\sum_{j \in K} p_j \cdot \lambda_j(\hat{x}^K) > 0 \,. \tag{5}$$

In the same paper he describes a linear programming algorithm that can be used to test whether such a vector p exists.

Cooperative behavior and in particular permanence have been shown to be rather rare events in random networks: the probability of permanence is smaller than 4^{-n} if i.i.d. coupling constants a_{ij} are assumed (Stadler & Happel, 1993). We have also estimated the probability that a randomly generated permanent network incorporates an additional species such that the resulting network is again permanent. These incorporation frequencies decrease also exponentially with the size of the catalytic network. In fact, the chance to reach large permanent networks by stepwise incorporation of random "invaders" is orders of magnitudes smaller than the chance that a randomly assembled network is permanent.

This picture changes dramatically for the evolved replicator networks. We have tested roughly 10^6 interaction matrices sampled from mutation using Jansen's (Jansen, 1986) linear programming algorithm as a sufficient condition for permanence. The computer code for the linear programming was taken from the NAG-package. The result was surprising: Every single tested interaction matrix was *permanent*. The formation of dynamically stable coexistence thus seems to be a by-product of the slow evolution of the replicator networks through iterated incorporation of mutants.

2.5. Survival Times

Besides the number of living species, the survival "time" of a species in an evolving replicator network is of interest. We define the survival time as the number of invasion attempts that a network suffers between the creation of species and its extinction. Figure 5 shows that most species are short-lived. Some species, however, manage to survive hundreds of cycles. The data show exponentially decreasing tails.

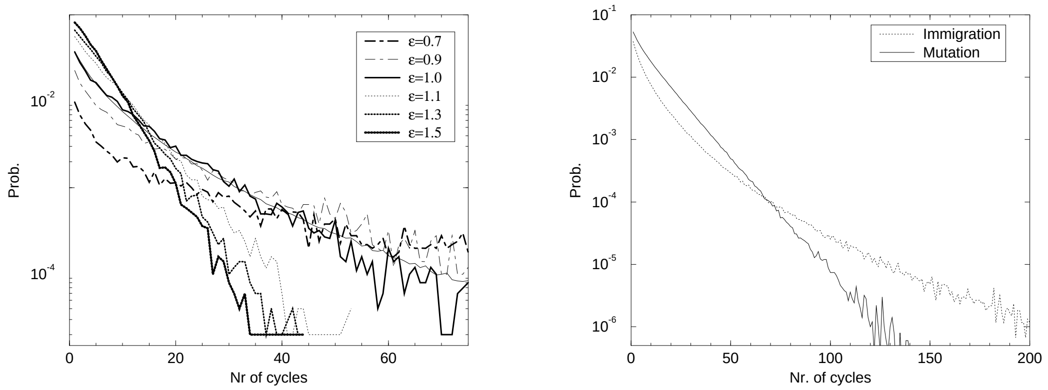

Figure 5: Probability of a species to survive a certain number of cycles.
L.h.s.: Dependence of the survival time on the interaction strength ϵ in the immigration model.
R.h.s.: Comparison of mutation model and immigration model with $\epsilon = 1$.

Again we find that the survival times in the mutation model are independent of the size of the mutations. In the immigration model, on the other hand, the interaction strength is of crucial importance.

3. Discussion

The perturbation of a given catalytic network can occur in two different ways: immigration and mutation. An immigrant is a species that is unrelated to the species in the network. Hence we model its interaction with the network species using i.i.d. randomly distributed interaction coefficient. On the other hand, a mutant is obtained from a parent-species in the networks by (slightly) perturbing its interactions with all other species. We find that the magnitude of these perturbations has no qualitative influence on the long term dynamics.

In intruder, be it a mutant or an immigrant, can cause three scenarios:

(i) The intruder in incorporated into the network, which grows from size n to size $n+1$. This is a rare event, and it becomes even less likely when the existing network is large already.

(ii) The frequency of the invader grows initially, but it is expelled after some time. The size of the network remains unchanged.

(iii) The invader causes the extinction of one of the previously coexisting species. A mutant might just replace its ancestor in the network, or it may destroy the entire network. The behavior of mutants and immigrants is significantly different in this case: mutants tend to kill only a moderate fraction of the network, in many cases they only super-seed their parent species, while immigrants often out-compete the entire network.

Since immigrants have a non-zero chance of destroying the entire network, there is no long term growth of diversity (i.e., number of species) in this case. The relative size of the interaction with the existing network is crucial for the probability of a successful invasion of the new one. If, on the average, its size is much greater than the strength of the interactions among the old species, it will dominate the average fitness term and the chance to be successful will approach fifty percent. On the other hand, if there is not much interaction (e.g. because the immigrant does not find an inhabitable ecological niche in the invaded system) the probability of invasion decreases drastically.

Mutation leads to a slow increase of diversity consistent with a logarithmic increase of the number of species with the number of mutation events. The most striking observation, however, is that the networks that are produced by this mechanism are permanent, i.e., the coexistence of the surviving species is a robust property.

It is insensitive to finite perturbation of their relative concentrations. We also observe an increase of the average fitness (replication rate) in these networks.

However, individual replicator species are short-lived in our model. The distribution of survival times decreases exponentially both with mutation and immigration.

While we have shown that replicator networks can evolve to form moderately large robust ecosystems by incorporating a sequence of mutants, this mechanism, however, does not solve the *parasite problem* that was found to haunt hyper-cycles (Eigen & Schuster, 1979) parasites (in our case unrelated invaders) may destroy a cooperative replicator network. For detailed conditions on the structure of the interaction matrix $\mathbf{A}$, under which an invader is capable of destroying an otherwise permanent network see (Stadler & Schuster, 1996). The formation of spatially separated compartments still appears to be the only possibility to overcome the threat of parasitic invaders (Eigen & Schuster, 1979; Hogeweg, 1994).

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