

Phase Transition and $1/f$ Noise in a Game Dynamical Model

Manfred Opper and Sigurd Diederich

Institut für Theoretische Physik, Justus-Liebig-Universität Giessen, Giessen, Germany

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We study a population of interacting species, described by the *replicator model* well established in theoretical biology. Using methods of statistical physics we present an exact steady-state solution to the model as a function of the population's *cooperation pressure* u when the number of species is large and the interactions are taken as random. When u is lowered to a critical value u_c , the solution becomes unstable. This phase transition manifests itself by a $1/f$ behavior in the power spectrum of the system's response against weak external noise.

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Statistical physics of disordered systems has proven to be extremely useful in understanding the behavior of complex systems consisting of many entities which interact via competing interactions. Prominent examples of such systems are the neural network models of the brain, which have been extensively studied in the last years. Recently similar methods have been applied to the modeling of complex ecological systems [1-3]. An important problem in using the tools of disorder physics to study the latter models is that in general no equilibrium distribution similar to the Gibbs ensemble in physical systems is available to describe their steady-state behavior. Thus only systems with specific symmetries [2] or cases which are essentially equivalent to linear equations [3] have been solved so far. In this Letter we present solutions to a prominent model of ecology which lacks the aforementioned simplifications.

In this model the time development of populations of different species is described by a system of so-called *game dynamical differential equations*. The state of a population at time t is characterized by a vector of strategies $\mathbf{x} = (x_1, \dots, x_N)$ with x_i being the fraction of individuals playing strategy i ($x_i \geq 0$, $\sum_{i=1}^N x_i = N$). An animal adopting a strategy i in a population x receives a payoff f_i , which in the evolutionary game is identified with the number of offspring. f_i serves as a measure of success for strategy i .

If the offspring itself will inherit the same strategy the *temporal rate of increase* for the fraction of these animals can be set roughly proportional to the payoff f_i . Thus we will describe the time development of the entire

population by the following system of nonlinear differential equations:

$$\frac{d}{dt} x_i(t) = x_i(t) \left(f_i(t) - N^{-1} \sum_{j=1}^N x_j(t) f_j(t) \right), \quad (1)$$

$$i = 1, \dots, N.$$

The term $N^{-1} \sum_{j=1}^N x_j f_j$ guarantees that the densities x_i remain normalized, i.e., $\sum_{i=1}^N x_i = N$ for all times.

Equation (1) is usually referred to as the replicator equation [4]. It describes the evolution of self-replicating entities, replicators, in different disciplines of biological sciences, e.g., genetics, ecology, prebiotic evolution, and sociobiology [5,6].

In general, the payoff vector $\mathbf{f} = (f_1, \dots, f_N)$ itself will depend on the state \mathbf{x} . In the following we will study a simple ansatz,

$$f_i(t) = \sum_{j \neq i}^N (u - w_{ij}) x_j(t) = uN - u x_i(t) - \sum_{j=1}^N w_{ij} x_j(t), \quad (2)$$

which nevertheless can yield nontrivial and rich behavior of the system. The parameter $u > 0$ describes an average tendency of the individuals to cooperate [7]. Large "cooperation pressure" u [8] will favor states where all replicators are equally likely, whereas for small u only a few species will survive. w_{ij} describes (with $w_{ii} = 0$) the fluctuations from this average value. Equation (2) can be regarded as the first terms in a Taylor expansion of \mathbf{f} . We shall incorporate additional rapid environmental fluctuations by adding a noise term $\sigma \xi_i(t)$ to the fitness function f_i :

$$\frac{d}{dt} x_i(t) = -x_i(t) \left(u x_i(t) + \sum_{j=1}^N w_{ij} x_j(t) + \sigma \xi_i(t) - \lambda(t) \right), \quad i = 1, \dots, N. \quad (3)$$

For simplicity we assume that $\xi_i(t)$ is a Gaussian white noise, i.e., $\langle \xi_i(t) \xi_j(t') \rangle = \delta_{ij} \delta(t - t')$ and that (3) should be understood in the Stratonovich [9] sense. The term $\lambda(t) = -N^{-1} \sum_{j=1}^N x_j (f_j - uN + \sigma \xi_j)$ guarantees proper normalization.

Investigations of systems with small N and $\sigma = 0$ have shown that the symmetry properties of the matrix w_{ij} are important for the steady-state behavior of the model.

Whereas for a symmetric matrix $w_{ij} = w_{ji}$ a Lyapunov function exists in the noiseless case ($\sigma = 0$), allowing only for fixed point solutions at large times, limit cycles or even chaotic trajectories [10] may appear in the general nonsymmetric case.

In the following we are interested in systems where the number N becomes very large. In this limit it seems nat-

ural to study a model where the couplings w_{ij} are taken as time-independent random quantities. To be specific we assume that the w_{ij} 's are Gaussian random variables with zero mean and second moments $\langle w_{ij}^2 \rangle = N^{-1}$, $\langle w_{ij}w_{ji} \rangle = \eta N^{-1}$, and $\langle w_{ij}w_{kl} \rangle = 0$ if the pairs (ij) and (kl) are different. The scaling of the coupling strengths with N , the number of strategies, keeps the fitness functions f_i typically of order 1 for large N .

This ansatz for the couplings in (2) suggests that the model can be treated by mean-field methods of statistical physics, which become exact for $N \rightarrow \infty$. Unfortunately the noise-driven system (3) is not of the standard Langevin type studied extensively in physics. An integrability condition [11] which would provide us with an explicit stationary probability distribution is not available in our case. This is why well-known *static* methods of statistical physics such as the replica trick [12] cannot be applied.

We have to resort to a full *dynamical* mean-field theory which provides us with a stochastic single-species equation of motion. Such an equation is derived by dynamical functional methods [13] or more intuitively by means of so-called cavity methods introduced in [14]. Since the derivation of the mean-field equation in our case resembles much of the corresponding treatment for the spin-glass problem [13], we merely quote and interpret the result. Assuming that initially, at time $t = t_0$, the ecological system is described by a configuration where all x 's are nonzero [15] and statistically independent of the w_{ij} 's, we obtain (omitting the index i)

$$\frac{d}{dt}x(t) = -x(t) \left[ux(t) + \eta \int_{t_0}^t ds K(t,s)x(s) + \Phi(t) + \sigma \xi(t) - \lambda(t) \right]. \quad (4)$$

$$\frac{d}{dt}y(t) = -[x_\infty + y(t)] \left[ux_\infty + x_\infty \eta \int_{-\infty}^t K(t-s)ds - \lambda + \sqrt{q}z \right] - x_\infty \left[uy(t) + \eta \int_{-\infty}^t K(t-s)y(s)ds + v(t) + \sigma \xi(t) \right]. \quad (5)$$

Let us first discuss the case $\sigma = 0$. If the system approaches the fixed point x_∞ for $t \rightarrow \infty$, $y(t), v(t)$ vanish asymptotically and we obtain $x_\infty [x_\infty(u + \eta K_0) - \lambda + \sqrt{q}z] = 0$, with $K_0 = \int_0^\infty ds K(s)$. This equation allows for a *positive solution* x_∞ only if $\lambda - \sqrt{q}z > 0$ [16]. For $\lambda - \sqrt{q}z < 0$ we set $x_\infty = 0$. Both solutions are matched in

$$x_\infty(z) = (u + \eta K_0)^{-1} (\lambda - \sqrt{q}z) \Theta(\lambda - \sqrt{q}z), \quad (6)$$

where $\Theta(x)$ is the unit step function. The asymptotic probability density $p(x)$ of the concentrations x of the species becomes a sum of two terms $p_+(x_\infty)$ and $p_0(x_\infty)$ where $p_0(x_\infty) = (1 - \alpha)\delta(x_\infty)$ describes a *finite fraction* $1 - \alpha$ of species which die out at large times. From (6) we easily obtain $\alpha = \int_{-\infty}^\Delta Dz$, where $Dz = (2\pi)^{-1/2} \times \exp(-\frac{1}{2}z^2)dz$ is the normalized Gaussian measure and $\Delta = \lambda/q^{1/2}$. Using the self-consistency conditions $\langle x_\infty^2 \rangle = q$ and $K_0 = q^{-1/2} \langle \partial x_\infty / \partial z \rangle$ together with the nor-

In place of the random interactions $w_{ij}x_j$ with the other species, a retarded self-interaction $K(t,s)x(s)$ appears together with a Gaussian noise $\Phi(t)$. $K(t,s)$ results from the "polarization" [14] of all other $x_j(t)$'s due to the presence of $x_i(s)$ at previous times $s < t$. It is given by the functional derivative $K(t,s) = \langle \delta x(t) / \delta \Phi(s) \rangle$ where $\lambda(t)$ has to be kept fixed upon differentiation. Causality requires that $K(t,s) = 0$ for $s > t$. Φ is a Gaussian colored noise with zero mean. It describes the non-coherent part of the interaction. Its covariance must be determined self-consistently through $\langle \Phi(t)\Phi(t') \rangle = \langle x(t)x(t') \rangle$. Finally $\lambda(t)$ has to be adjusted so that the average of x is normalized to $\langle x(t) \rangle = 1$.

The appearance of the colored noise together with the memory makes a general solution of (4) impossible. In this Letter we present a steady-state solution in the limit of weak external noise. We expect that at least for a large enough u and $\sigma = 0$ the system might approach a fixed point $x_{i,\infty}$ as $t \rightarrow \infty$. How can such a result emerge from the single-species equation (4)? A fixed point of (4) must still be a *random variable*, displaying the stochastic variation of $x_{i,\infty}$ on the number i . We thus try the ansatz $x(t) = x_\infty + y(t)$, for large times $t \gg t_0$, where $y(t)$ is a small deviation from the fixed point x_∞ . Likewise we set $\Phi(t) = \sqrt{q}z + v(t)$, where z is a static Gaussian of unit variance and v is a small dynamic component. We also make the crucial assumption that for large times the system will completely lose its memory from the initial state $x(t_0 = -\infty)$, so that dynamical correlations and the kernel $K(t,s)$ will only depend on time differences $t - s$. If σ is small enough so that the system will stay in the vicinity of the fixed point we will keep terms up to linear order in $y(t)$ and $v(t)$ in Eq. (4). Neglecting all effects from transient states we obtain

malization $\langle x_\infty \rangle = 1$ we derive the explicit relations

$$\begin{aligned} (u + \eta K_0)^2 &= \int_{-\infty}^\Delta Dz (\Delta - z)^2, \\ K_0 &= -\frac{u}{2\eta} + \left[\frac{u^2}{4\eta^2} - \frac{\alpha}{\eta} \right]^{1/2}, \\ (u + \eta K_0) &= \sqrt{q} \int_{-\infty}^\Delta Dz (\Delta - z). \end{aligned} \quad (7)$$

Equation (7) can be solved for Δ , q , and K_0 in the entire parameter range $u > 0$ and $-1 \leq \eta \leq 1$ exhibiting no kind of discontinuities. As expected one finds that the fraction of surviving species is an increasing function of the cooperation tendency u for each η .

One might question whether the fixed point (6) represents the generic asymptotic solution of our replicator system. In fact, recent studies of random network models (see, e.g., Refs. [17,18]) with asymmetric ($\eta = 0$) cou-

plings have shown that there the dynamics is typically *chaotic*. Though we are not able at present to prove in which cases our static solution is *globally* attractive, we will discuss its *local* stability by including the small perturbations $y(t)$. We begin with the species which become extinct for large times, i.e., $x_\infty=0$. In this case Eq. (5) reduces to $\dot{y}(t)=y(t)(\lambda-\sqrt{q}z)$, where the overdot is an abbreviation for the time derivative. From the previous assumption, $\lambda-\sqrt{q}z < 0$, we find that fluctuations are in fact exponentially damped. Note that the external noise $\sigma\xi(t)$ does not affect this result in linear order.

Next we solve for the small oscillations around the positive components $x_\infty > 0$ via a Fourier transform of (5),

$$y(\omega) = -\frac{x_\infty(z)[v(\omega) + \sigma\xi(\omega)]}{i\omega + x_\infty(z)[u + \eta K(\omega)]} \tag{8}$$

$$C(\omega) \approx \sigma^2 \left[\frac{\alpha}{K_0^2} - 1 + |\omega| \pi p_+(0) \left\{ \frac{\mu}{\alpha(u + 2\eta K_0)} - \frac{1}{2K_0\alpha} \right\} \right]^{-1} \tag{10}$$

This yields a slow decay of the correlations $C(t) \propto t^{-2}$ for all $u > u_c = (1/\sqrt{2})(1 + \eta)$, suggesting that at least trajectories in the vicinity of the fixed point will be attracted by it for $u > u_c$. In fact, numerical solutions of the replicator system show *generic convergence* to the static solution from random initial conditions in this range of parameters. If $u = u_c$ and $\eta < 1$ the first term of $C(\omega)$ in (10) vanishes, whereas the second remains finite, leaving us with a diverging $C(\omega) \propto |\omega|^{-1}$ [19]. The appearance of this $1/f$ noise signals that the static solution (6) becomes unstable. This slow relaxation of fluctuations $C(\omega)$ is displayed in Fig. 1 for $\eta=0$, noise strength $\sigma^2=0.02$, and $u=0.72$, which is slightly above the critical value u_c . For $u < u_c$ and all η , $C(\omega=0)$ as obtained in (10) would become negative, showing that our solution cannot be continued to the region $u < u_c$.

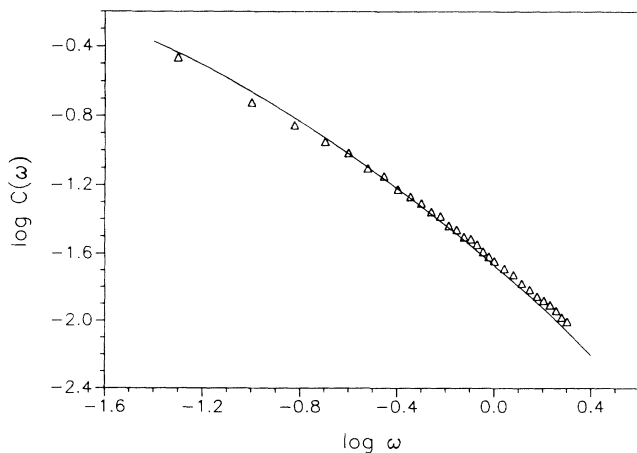


FIG. 1. Logarithmic plot of $C(\omega)$, Eq. (9) for $\eta=0$, noise strength $\sigma=0.02$, and $u=0.72$ slightly above the critical value $u_c=1/\sqrt{2}$. The triangles are obtained from simulations of the system (3) for the same values of parameters and $N=800$ species averaged over fifty samples.

The self-consistency relation

$$C(t) = \langle y(t)y(0) \rangle = \langle v(t)v(0) \rangle$$

for the power spectrum $C(\omega)$ yields

$$C(\omega) = \langle |y(\omega)|^2 \rangle = \sigma^2 \left[\frac{1}{\langle |i\omega/x_\infty + u + \eta K(\omega)|^{-2} \rangle_+} - 1 \right]^{-1}, \tag{9}$$

where a threefold average over the dynamic noise terms $v(t)$ and $\xi(t)$ together with the static noise z has been performed. $K(\omega) = \int_{-\infty}^{\infty} dt e^{i\omega t} K(t)$ is determined via $K(\omega) = \langle \partial y(\omega) / \partial v(\omega) \rangle$. The limit of $C(\omega)$ for small ω determines the long-time decay of the correlations $C(t)$. We find

This dynamical transition can be related to instabilities of simpler models for large ecosystems which have been studied in recent years [20,21]. Such systems were modeled by *linear* differential equations with a large random matrix. The instability occurs when the real part of its first eigenvalue becomes negative. To understand the relationship with our work we linearize the original replicator system (3) around the asymptotic fixed points $x_{i,\infty}$ keeping only the surviving species $i=1, \dots, aN$ (after renumbering). This yields the linear system

$$\frac{d}{dt} y_i(t) = -x_{i,\infty} \left[\sum_{j=1}^{aN} A_{ij} y_j(t) + \sigma\xi_i(t) \right], \tag{11}$$

where $A_{ij} = u\delta_{ij} + w_{ij}$ and $y_i(t) = x_i(t) - x_{i,\infty}$. Using a result of Sommers *et al.* [22] on the spectrum of large random matrices with fixed symmetry η we find for the minimum real part a_{\min} of the eigenvalues of A that $a_{\min} = u - \sqrt{\alpha}(1 + \eta)$. $a_{\min} = 0$ is the value where small fluctuations are no longer damped. Inserting $\alpha = \frac{1}{2}$, which is the fraction of surviving species at the transition, from our dynamical theory we gain the correct value $u = u_c = (1/\sqrt{2})(1 + \eta)$ for the critical parameter. With a proper redefinition of interaction strengths, dimension of the matrix, etc., we recover the instability condition obtained in [20,21] from numerical investigations. The main difference from this work lies in the fact that in their approach the number aN of (surviving) species was given and fixed *a priori*. On the other hand, within the replicator approach these species are selected *dynamically*.

Though our present approach fails to describe the steady-state behavior of the ecological model for $u < u_c$ we would like to present a few ideas about the behavior in this region.

The breakdown of our static solution (6) does not ex-

clude the possibility of other fixed point solutions. In fact, for $\eta=1$, $\sigma=0$ all trajectories evolve into fixed points irrespective of the value of u . The failure of our ansatz to account for such solutions is most probably due to the assumption of a unique equilibrium state which is reached independently of the initial conditions. Deviations from such a simple behavior are well known for complex systems such as the Sherrington-Kirkpatrick model of spin glasses [23,24]. For large N its phase space becomes divided into many ergodic components each of which the system can escape only in times diverging exponentially with N . In the dynamical approach one has to account properly [25] for the initial conditions in order to recover equilibrium results. We expect a similar complex picture to hold for $\eta \approx 1$ and $u < u_c$. This assumption is supported by a calculation of the average number \mathcal{N} of stable fixed points of Eq. (3) with $\eta=1$ [2,26]. For $u > u_c$ we found a single fixed point, which becomes marginally stable for $u = u_c$. For $u < u_c$, an exponentially large number, $\mathcal{N} \propto e^{\gamma N}$ with $\gamma > 0$, of marginally stable fixed points is calculated. Simulations of the replicator equations in this region show in fact a distribution of fixed points which asymptotically evolve from different random initial conditions.

We expect a different picture to be valid if η is sufficiently small. For $\eta=0$ and $u < u_c$, we got $\mathcal{N} \propto e^{\gamma N}$ with $\gamma < 0$, i.e., no stable fixed point could be found [26]. This fact and preliminary simulations strongly suggest that similar to the aforementioned network models [17,18] the ecosystem may now rather end in a chaotic attractor. This change of behavior would be similar to the freezing transition in asymmetric random spin models [18,27,28].

Our results indicate that the replicator model can exhibit an interesting complex behavior. This will be tested in further work using large-scale computer simulations together with a new method to treat dynamical mean-field equations numerically [29].

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