

Random Replicators with High-Order Interactions

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We use tools of the equilibrium statistical mechanics of disordered systems to study analytically the statistical properties of an ecosystem composed of N species interacting via random mutual interactions, as well as via deterministic self-interactions of order $p \geq 2$. We show that the main effect of increasing the order of the interactions among the species is to make the system less competitive, in the sense that the fraction of extinct species is greatly reduced. In addition, we find that for $p > 2$ there is a threshold value which gives a lower bound to the concentration of the surviving species, preventing then the existence of rare species and, consequently, increasing the robustness of the ecosystem to external perturbations.

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Conservationists' arguments in favor of biodiversity have often appealed to the existence of intricate ties among apparently unrelated species in which, for instance, the strengths of the interactions between any pair of species would depend on the concentrations or frequencies of a variety of different ones [1]. Although the roles played by the total number of species, as well as by the strengths of their pairwise interactions, in the stability of an ecosystem are now fairly well understood both theoretically and experimentally [2–4], it is still not clear whether high-order interactions among the species would actually bring any advantage, in the sense of a larger robustness, to the ecosystem. This is the main issue we address in this Letter. Albeit the model proposed here is somewhat unrealistic from the biological viewpoint, since its dynamics is governed by a Lyapunov function, it clearly points out the advantages of high-order interactions, making clear-cut, nontrivial predictions, such as the reduction of the number of extinct species and the existence of a concentration threshold which excludes rare species from the ecosystem at equilibrium.

Traditionally, the study of coevolution of species has been restricted to deterministic interactions [5]; however, the ever-present uncertainties about how the species are actually interacting combined to the overwhelming complexity of those interactions [4] motivate an alternative, and perhaps complementary, approach in which the strengths of the interactions between the species are assigned at random. In this Letter we solve analytically a model of coevolution of N species interacting via random, high-order interactions. Our model is a generalization of the random replicant model [6–8] which considers only pair interactions between the species.

We consider an infinite population (ecosystem) composed of individuals belonging to N different species whose fitness \mathcal{F}_i ($i = 1, \dots, N$) are the derivatives $\mathcal{F}_i = \partial \mathcal{F} / \partial x_i$ of the fitness functional \mathcal{F} defined as

$$-\mathcal{F} = \mathcal{H}_p(\mathbf{x}) = u \sum_i x_i^p + \sum_{1 \leq i_1 < i_2 < \dots < i_p \leq N} J_{i_1 i_2 \dots i_p} x_{i_1} x_{i_2} \dots x_{i_p}, \quad (1)$$

where x_i is the concentration of species i . These variables satisfy the constraints

$$\sum_{i=1}^N x_i = N \quad (2)$$

and $x_i \geq 0 \forall i$. Here the coupling strengths are statistically independent random variables with a Gaussian distribution

$$\mathcal{P}(J_{i_1 i_2 \dots i_p}) = \sqrt{\frac{N^{p-1}}{\pi p!}} \exp\left[-\frac{(J_{i_1 i_2 \dots i_p})^2 N^{p-1}}{p!}\right] \quad (3)$$

for $i_1 < i_2 < \dots < i_p$. The self-interaction parameter $u \geq 0$ acts as an external cooperation pressure limiting the growth of any single species, and it is crucial to guarantee the existence of a nontrivial thermodynamic limit, $N \rightarrow \infty$. The interesting features of the model stem from the competition between the deterministic diagonal and the random off-diagonal terms in $\mathcal{H}_p(\mathbf{x})$: on the one hand, the random mutual interactions favor the existence of only a few species coupled via large negative coupling strengths $J_{i_1 i_2 \dots i_p}$, while, on the other hand, the positive self-interaction terms favor the coexistence of all species at the lowest possible concentrations. It is convenient to think of u as a measure of the relative strength between the self- and the mutual interactions, so that the limit $u \rightarrow \infty$, for which the equilibrium solution is $x_i = 1 \forall i$, corresponds to the situation where there is no mutual interaction. Hence decreasing the value of u allows us to investigate how the gradual introduction of mutual interactions destabilizes that regime of perfect coexistence among the species.

It can be shown that the dynamics

$$\frac{dx_i}{dt} = -x_i \left[\frac{\partial \mathcal{H}_p}{\partial x_i} - \frac{1}{N} \sum_k x_k \frac{\partial \mathcal{H}_p}{\partial x_k} \right] \quad \forall i \quad (4)$$

minimizes $\mathcal{H}_p(\mathbf{x})$ while the total concentration $\sum_i x_i$ is a constant of motion (see, e.g., Ref. [5], p. 240). This type of first-order differential equation, termed replicator equation, has been used to describe the evolution of self-reproducing entities (replicators) in a variety of fields, such as game theory, prebiotic evolution, and sociobiology, to name only a few [9]. In particular, a fourth-order interactions replicator equation was shown to govern the game

dynamics in Mendelian (sexual) populations [10]. For the sake of simplicity, in writing the fitness functional, Eq. (1), we have implicitly assumed that the couplings $J_{i_1 i_2 \dots i_p}$ are invariant under permutations of the indices i_1, \dots, i_p . We must stress, however, that regardless of whether the couplings are invariant or not, the interaction term in the replicator equation, namely, $\partial \mathcal{H}_p / \partial x_i$, will be invariant to permutations of the species indices, and so the dynamics will converge to a fixed point. In this sense, the mere existence of a fitness functional (Lyapunov function) is a severe assumption from the biological viewpoint. On the other hand, it allows full use of the tools of the equilibrium statistical mechanics to study analytically the properties of the fixed points of the corresponding replicator equation.

In the sequel we present the results of the replica analysis of the statistical properties of the ground state of the multispecies interaction Hamiltonian (1). Following the standard prescription of performing quenched averages on extensive quantities only [11], we define the average free-energy density f as

$$-\beta f = \lim_{N \rightarrow \infty} \frac{1}{N} \langle \ln Z \rangle, \quad (5)$$

where

$$Z = \int_0^\infty \prod_j dx_j \delta\left(N - \sum_j x_j\right) e^{-\beta \mathcal{H}_p(\mathbf{x})} \quad (6)$$

is the partition function and $\beta = 1/T$ is the inverse temperature. Taking the limit $T \rightarrow 0$ in Eq. (6) ensures that only the states that minimize $\mathcal{H}_p(\mathbf{x})$ will contribute to Z . Here $\langle \dots \rangle$ stands for the average over the coupling strengths. As usual, the evaluation of the quenched average in Eq. (5) can be carried out through the replica method [11]. Within the replica-symmetric framework we find that, in the thermodynamic limit, the average ground-state energy per species is given by

$$\epsilon_0 = \lim_{\beta \rightarrow \infty} f = u \int_{-\infty}^{\gamma} Dz x_s^p(z) - \frac{p}{2} y q^{p-1}, \quad (7)$$

where $Dz = dz \exp(-z^2/2)/\sqrt{2\pi}$ is the Gaussian measure,

$$\gamma = (p-2)q^{\frac{p-1}{2}} \left(\frac{1}{u}\right)^{\frac{1}{p-2}} \left(\frac{y}{2}\right)^{\frac{p-1}{p-2}} \left(\frac{p}{2}\right)^{\frac{p}{2(p-2)}} - \Delta, \quad (8)$$

and $x_s(z)$ is the positive solution of

$$\frac{1}{2} p(p-1) y q^{p-2} x_s - p u x_s^{p-1} - \left(\frac{p}{2} q^{p-1}\right)^{1/2} (\Delta + z) = 0, \quad (9)$$

which maximizes the effective Hamiltonian

$$\Xi_x = \frac{1}{4} p(p-1) y q^{p-2} x^2 - u x^p - \left(\frac{p}{2} q^{p-1}\right)^{1/2} (\Delta + z) x. \quad (10)$$

We note that $x_s(z) = 0$ for $z > \gamma$. Here the saddle-point parameters q , y , and Δ are given by the equations

$$1 = \int_{-\infty}^{\gamma} Dz x_s(z), \quad (11)$$

$$q = \int_{-\infty}^{\gamma} Dz x_s^2(z), \quad (12)$$

and

$$y p |p-1| = \int_{-\infty}^{\gamma} Dz \frac{1}{|\frac{1}{2} y q^{p-2} - u x_s^{p-2}(z)|}. \quad (13)$$

Although in general these equations can be solved numerically only, we can easily obtain an analytical solution for large u :

$$q \approx 1 + \frac{1}{u^2} \frac{1}{2p(p-1)^2}, \quad (14)$$

$$y \approx \frac{1}{u} \frac{1}{p(p-1)} \left[1 + \frac{1}{u^2} \frac{1}{4(p-1)} \right], \quad (15)$$

$$\Delta \approx -u(2p)^{1/2} \left[1 - \frac{1}{u^2} \frac{p+1}{4p(p-1)} \right]. \quad (16)$$

The physical order parameter q is defined by [11]

$$q = \left\langle \frac{1}{N} \sum_i \langle x_i \rangle_T^2 \right\rangle, \quad (17)$$

where $\langle \dots \rangle_T$ stands for a thermal average taken with the Gibbs probability distribution

$$\mathcal{W}(\mathbf{x}) = \frac{1}{Z} \delta\left(N - \sum_j x_j\right) \exp[-\beta \mathcal{H}_p(\mathbf{x})]. \quad (18)$$

Hence, values of q on the order of 1 indicate the coexistence of a macroscopic number of species, while large values of q signalize the dominance of a few species (i.e., the number of surviving species is on the order of N^α with $\alpha < 1$) only. In Fig. 1 we present the physical order parameter q as a function of the cooperation pressure u for several values of p . As expected, for large u the ecosystem is cooperative, in the sense that almost all species survive, and so $q \approx 1$. For small u the system enters a strongly competitive regime characterized by the divergence of q , though the onset of this regime can be postponed by increasing the order of the interactions p , as illustrated in Fig. 1. Interestingly, the analysis of the effective Hamiltonian (10) for $u = 0$ shows that x_s and consequently q [see Eq. (12)] are finite only for $p < 1$, which corresponds to a random version of Szathmáry's model of parabolic growth [12,13]. As the divergence of q signals the survival of only a few species, the finitude of q at $u = 0$ is consistent with a parabolic growth for which the coexistence of all species is assured.

To understand better the distribution of species in the ground state we calculate the distribution of probability

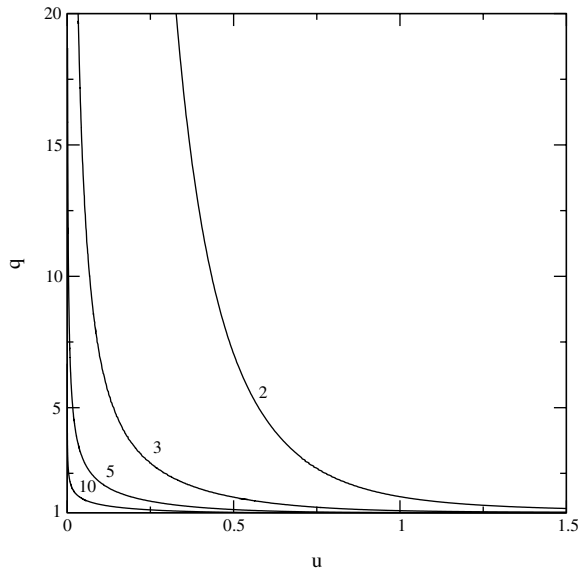


FIG. 1. Physical order parameter q as a function of the cooperation pressure u for $p = 2, 3, 5,$ and 10 .

that a certain species concentration, say x_k , assumes the value x , defined by

$$\mathcal{P}_k(x) = \lim_{\beta \rightarrow \infty} \left\langle \int_0^\infty \prod_j dx_j \delta(x_k - x) \mathcal{W}(\mathbf{x}) \right\rangle \quad (19)$$

with $\mathcal{W}(\mathbf{x})$ given by Eq. (18). Since all species concentrations are equivalent we can write $\mathcal{P}_k(x) = \mathcal{P}(x) \forall k$. Moreover, to handle a possible singularity in the limit $\beta \rightarrow \infty$ it is more convenient to consider instead the cumulative distribution function $C(x) = \int_0^x dx' \mathcal{P}(x')$. Carrying out the calculations we obtain

$$C(x) = \int_\gamma^\infty Dz + \int_{-\infty}^\gamma Dz \Theta[x - x_s(z)], \quad (20)$$

where $\Theta(x) = 1$ for $x > 0$ and 0 otherwise. For $u \rightarrow \infty$ we find $C(x) = \Theta(x - 1)$ regardless of the value of p since in this case the equilibrium solution is $x_i = 1 \forall i$. An interesting feature of the cumulative distribution function is that $C(0)$ is nonzero, indicating thus that the probability distribution $\mathcal{P}(x)$ has a delta peak at $x = 0$. In fact, the first term of the right-hand side of Eq. (20), i.e., $C(0)$, yields the fraction of extinct species in the ground state. In addition, as shown in Fig. 2, the constancy of $C(x)$ up to a threshold concentration value $x_t = x_s(\gamma)$ indicates that there is a lower bound to the concentration of any surviving species. As illustrated in Fig. 3, x_t decreases monotonically with the cooperation pressure u ; its dependence on the order p of the interactions, however, is more complicated: while x_t decreases with increasing p for small u , it increases with p for large u . Glancing at Fig. 2 one can readily realize that the nature of the concentration threshold x_t is totally distinct from that of the threshold obtained in the limit $u \rightarrow \infty$, which equals 1 for all p . As expected, $x_t \rightarrow \infty$ for $u = 0$ since $C(x) = 1$ for all x in this limit, while

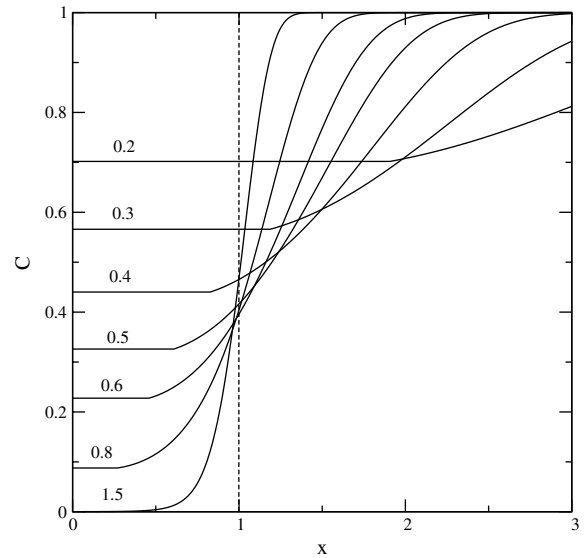


FIG. 2. Cumulative distribution function of the ground-state species concentrations for $p = 3$ and several values of u as indicated in the figure. The dashed line is the result for $u \rightarrow \infty$.

$$x_t \approx (2pu^2)^{-1/(p-2)} \quad p > 2 \quad (21)$$

for u large. Hence the concentration threshold disappears in the case that the self-interaction term becomes too dominant. A nonzero value of x_t is then an emergent property of ecosystems with high-order interactions ($p > 2$), which results from the nontrivial interplay between the self- and the mutual interactions. We note that $x_t = 0$ for any finite value of u in the case of pairwise interactions ($p = 2$). Of course, the existence of such a threshold has far-reaching consequences on the stability and robustness of the population against external perturbations since it implies the absence of rare, and hence prone to extinction, species

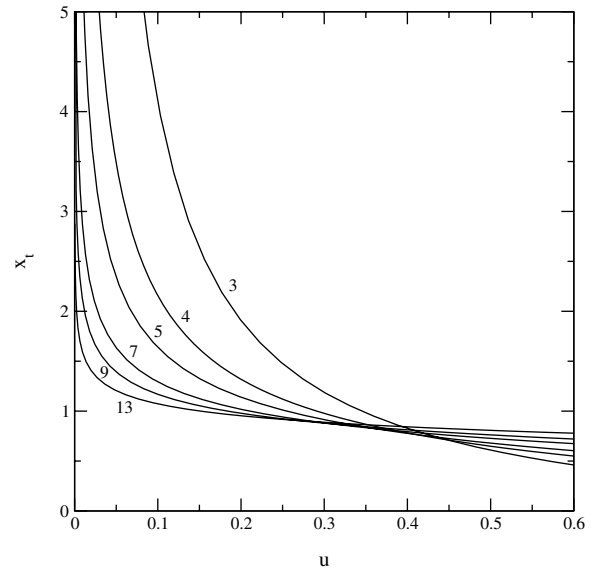


FIG. 3. Concentration threshold x_t as a function of u for $p = 3, 4, 5, 7, 9,$ and 13 . Note that $x_t = 0$ for $p = 2$.

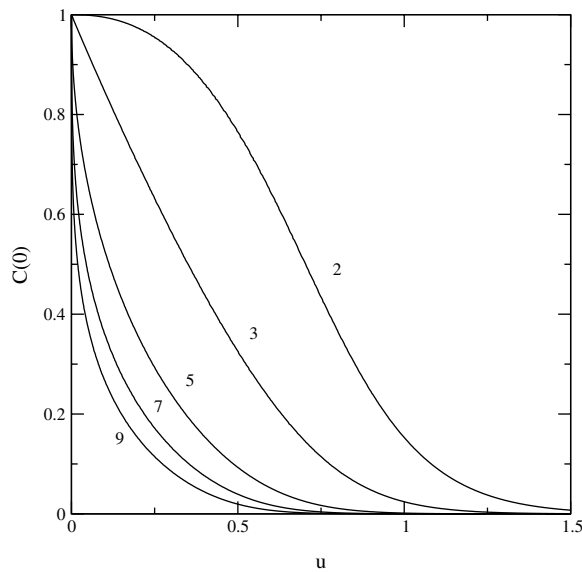


FIG. 4. Fraction of extinct species in the ground-state $C(0)$ as a function of u for several values of p as indicated in the figure. Note that $C(0) = 1$ for $u = 0$ indicating that only a few species survive in the thermodynamic limit.

whose loss might cause drastic effects in the whole population [2]. Furthermore, for fixed u the fraction of extinct species decreases exponentially with increasing p (see Fig. 4). Explicitly, for large u we find

$$C(0) \approx \frac{1}{(4\pi p)^{1/2}} \frac{1}{u} \exp(-pu^2), \quad (22)$$

which shows that increasing the order of the interactions among the species makes the ecosystem less competitive, thus corroborating the conclusions drawn from the analysis of Fig. 1.

We have verified the validity of the replica-symmetric solution by performing the standard stability analysis [14]. In particular, that solution becomes unstable for u smaller than $1/\sqrt{2} \approx 0.707$ and 0.106 for $p = 2$ and 3, respectively, while for $p \geq 4$ we find that it is unstable only at $u = 0$. Hence our main results are not affected by the (local) instability of the replica-symmetric solution.

Some remarks on the role of the high-order self-interaction terms $u \sum_i x_i^p$ are in order. As signaled by the divergence of the order parameter q for small values of u (Fig. 1), the concentrations of a few species become very large in this regime and so, in order to have a non-trivial interplay between the two antagonistic terms in the Hamiltonian (1), namely, the self- and the mutual interaction terms, the former must also be of higher order p . In fact, a similar study of the much simpler case, in which

the self-interaction terms are quadratic (i.e., $u \sum_i x_i^2$) but the mutual interactions are of higher order $p > 2$, corroborates that assertion. For instance, we found that for $p = 3$ the saddle-point equations have no solution (and so $q \rightarrow \infty$) already for $u < 2.028$ and, in addition, the range of this unphysical region increases linearly with increasing p .

To conclude we must emphasize that our results describe the equilibrium properties of the ecosystem only. Important issues such as whether the absence of rare species at equilibrium would imply that the ecosystem is stable with respect to the invasion of rare mutant species, or whether the effect of a perturbation decreasing the concentration of a single species to a value below x_i would lead to the collapse of the entire ecosystem, can be addressed only through a dynamical approach [8], which is beyond the scope of our present work. We hope the nontrivial predictions of our model will provide motivation for the proposal of more realistic models of high-order multispecies interactions.

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