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Replicators with Hebb interactions

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Abstract. We do an analytical study of the statistical properties of an ecosystem composed of species that are coupled *via* pairwise interactions that are given by the Hebb rule and have deterministic self-interactions u. In the model each species is characterized by an infinite set of $p = \alpha N$ traits. As one of our main results, we observe that the ecosystem becomes less cooperative as the complexity of species (number of traits) is increased.

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1 Introduction

The understanding of the nature of the complex interactions between species is of great importance to the study of ecosystems' functioning. As well as the interactions, the species composition also plays an important role in the dynamics and functioning of the system. Previous investigations show that the differences among traits of species can have large impacts on processes taking place in ecosystems [1]. In this contribution, we consider an ecosystem model where the interactions between species take into account the degree of their similarity. This is done by assuming a Hebb-like rule for the interactions between species.

The statistical mechanics of disordered systems has been very useful in the investigation of the behavior of complex systems consisting of many interacting species. In that approach, the models assume that the fitness of the species are a function of the interactions among individuals. In this context, the deterministic replicator models are used to investigate the coevolution of self-replicating entities in a variety of fields such as ecology, game theory and sociobiology [2]. An alternative approach that considers random interactions, the random replicator model, was developed by Diederich and Opper [3,4]. The dynamics of the model is governed by a Lyapunov function such that the only stationary states are fixed points. However, the model permits the use of tools developed in equilibrium statistical mechanics to obtain analytically the average properties of the equilibrium states of the disordered system.

Previous works about the random replicator model usually suppose interactions among species to be statistically independent random variables with Gaussian distribution [3–5]. In a more recent analysis, de Oliveira and Fontanari [6] studied the model taking into account a non-random structure for the interactions among species. They assumed that each species is characterized by a finite set of binary traits and then the resulting couplings between pairs of species depend on their traits according to a complementarity principle. Moreover, a bias parameter that favors one of the traits is introduced. In this contribution, we also assume a non-random structure in the interactions among species, but instead of dealing with a finite number of traits defining each species, here each species is characterized by an infinite set of binary traits.

The remaining of the paper is organized as follows. We introduce the model in Section 2. In the following section we use the replica approach to evaluate the average free-energy density in the thermodynamic limit, and also to derive the replica-symmetric order parameters. The stability analysis of the replica-symmetric solution is also carried out. In Section 4 we show our results for the probability distribution of the concentrations of species. And finally, we present the concluding remarks.

2 Model

In this model, the ecosystem is composed of an infinite number N of distinct species, where $x_i \in [0, \infty)$ denotes the concentration of individuals of species i $(i = 1, \dots, N)$. Each species is then represented by a set of p traits, ξ_i^μ, $\mu = 1, \dots, p$. The interaction between each pair of species depends on these traits according to a complementarity principle. We also assume that the number of traits p is proportional to ecosystem size N, i.e., $p = \alpha N$, where $\alpha \in [0, 1]$. Furthermore, the traits are quenched, independent random variables that can take on values $+1$ and -1 with probability $1/2$.

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The fitness $\mathcal{F}_i$ of each species i is taken as the derivative $\mathcal{F}_i = \partial\mathcal{F}/\partial x_i$, where the fitness function $\mathcal{F}$ is calculated as

$$-\mathcal{F} = \mathcal{H}(\mathbf{x}) = \sum_{i<j} J_{ij} x_i x_j + u \sum_i x_i^2. \tag{1}$$

Here, the coupling strength J_{ij} between species i and j is given by the Hebb rule

$$J_{ij} = \frac{1}{2N} \sum_{\mu=1}^{p} \xi_i^\mu \xi_j^\mu \quad i \neq j, \tag{2}$$

which was extensively used within the context of neural networks [7]. Since we wish to maximize the fitness function, that corresponds to minimizing $\mathcal{H}(\mathbf{x})$, $J_{ij} < 0$ corresponds to pairs of cooperating species, whereas $J_{ij} > 0$ to pairs of competing species. Therefore, the larger the number of complementary traits (*i.e.*, $\xi_i^\mu \xi_j^\mu = -1$), the more cooperative the pair of species. The notion of complementarity in ecology has gained importance since empirical observations show that complementary niches are more efficient in the use of the resources of the environment than monocultures [8].

The self-interaction parameter $u \geq 0$ in equation (1) guarantees the existence of a non-trivial thermodynamic limit, $N \to \infty$. It plays the role of a cooperation pressure that limits the growth of any single species. The meaning of positive self-interactions is that individuals of the same species compete against themselves for the available resources.

The concentrations of surviving species must satisfy the constraint

$$\sum_{i=1}^{N} x_i = N, \tag{3}$$

which introduces an additional source of competition among the species.

The concentrations x_i evolve in time according to the replicator equation

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = -x_i \left[\frac{\partial\mathcal{H}(\mathbf{x})}{\partial x_i} - \frac{1}{N} \sum_k x_k \frac{\partial\mathcal{H}(\mathbf{x})}{\partial x_k} \right] \qquad \forall i, \tag{4}$$

which minimizes $\mathcal{H}(\mathbf{x})$ while the total concentration $\sum_i x_i$ is kept constant. Hence the fixed points of the equation are the minima of $\mathcal{H}(\mathbf{x})$. In the following we use the replica formalism to obtain analytical derivations for the statistical properties of the minima.

3 Replica approach

Since we have to perform quenched averages on extensive quantities, we define the average free-energy density f as

$$-\beta f = \lim_{N\to\infty} \frac{1}{N} \langle \ln Z \rangle, \tag{5}$$

where

$$\begin{aligned} Z = \int_0^\infty \prod_i \mathrm{d}x_i \delta\Big(N - \sum_i x_i\Big) \\ \times \exp\Bigg\{ -\beta \Bigg[\frac{1}{2} \sum_\mu \left(\frac{1}{\sqrt{N}} \sum_i \xi_i^\mu x_i \right)^2 \\ + \left(u - \frac{\alpha}{2} \right) \sum_i x_i^2 \Bigg] \Bigg\} \end{aligned} \tag{6}$$

is the partition function and $\beta = 1/T$ is the inverse temperature. Here $\langle \ldots \rangle$ stands for the average taken on the probability distribution

$$\mathcal{P}(\xi) = \prod_\mu \left[\frac{1}{2} \delta(\xi_i^\mu - 1) + \frac{1}{2} \delta(\xi_i^\mu + 1) \right]. \tag{7}$$

As usual, we evaluate the quenched average in equation (5) through the replica method using the identity

$$\langle \ln Z \rangle = \lim_{n\to 0} \frac{1}{n} \ln \langle Z^n \rangle, \tag{8}$$

where we find $\langle Z^n \rangle$ for integer n and analytically continue to $n = 0$. Using standard techniques, we obtain in the thermodynamic limit, $N \to \infty$,

$$\begin{aligned} -\beta f = \lim_{n\to 0} \frac{1}{n} \mathrm{extr} \Bigg\{ \sum_{\gamma<\delta} \hat{q}^{\gamma\delta} q^{\gamma\delta} + \frac{1}{2} \sum_\gamma \hat{Q}^\gamma Q^\gamma \\ - \beta \left(u - \frac{\alpha}{2} \right) \sum_\gamma Q^\gamma + \sum_\gamma \hat{R}^\gamma + \alpha \ln G_1(q^{\gamma\delta}, Q^\gamma) \\ + \ln G_2(\hat{q}^{\gamma\delta}, \hat{R}^\gamma, \hat{Q}^\gamma) \Bigg\}, \end{aligned} \tag{9}$$

where

$$\begin{aligned} G_1 = \int_{-\infty}^{\infty} \prod_\gamma \frac{\mathrm{d}\tilde{p}^\gamma \mathrm{d}p^\gamma}{\sqrt{2\pi}} \exp\Bigg\{ \mathrm{i} \sum_\gamma \tilde{p}^\gamma p^\gamma - \frac{\beta}{2} \sum_\gamma (p^\gamma)^2 \\ - \frac{1}{2} \sum_\gamma Q^\gamma (\tilde{p}^\gamma)^2 - \sum_{\gamma<\delta} q^{\gamma\delta} \tilde{p}^\gamma \tilde{p}^\delta \Bigg\} \end{aligned} \tag{10}$$

and

$$\begin{aligned} G_2 = \int_0^\infty \prod_\gamma \mathrm{d}x^\gamma \exp\Bigg\{ - \sum_{\gamma<\delta} \hat{q}^{\gamma\delta} x^\gamma x^\delta - \frac{1}{2} \sum_\gamma \hat{Q}^\gamma (x^\gamma)^2 \\ - \sum_\gamma \hat{R}^\gamma x^\gamma \Bigg\}. \end{aligned} \tag{11}$$

We evaluate the extremum in equation (9) over all saddle-point parameters $\hat{q}^{\gamma\delta}$, $q^{\gamma\delta}$, $\hat{Q}^\gamma$, Q^γ e $\hat{R}^\gamma$. The order parameters

$$q^{\gamma\delta} = \left\langle \frac{1}{N} \sum_{i=1}^{N} \langle x_i^\gamma \rangle_T \langle x_i^\delta \rangle_T \right\rangle \qquad \gamma < \delta, \tag{12}$$

and

$$Q^{\gamma} = \left\langle \frac{1}{N} \sum_{i=1}^{N} \left\langle (x_i^{\gamma})^2 \right\rangle_T \right\rangle \tag{13}$$

give the overlap between a pair of different equilibrium states $\mathbf{x}^{\gamma}$ and $\mathbf{x}^{\delta}$, and the overlap of the equilibrium state $\mathbf{x}^{\gamma}$ with itself, respectively. Here, $\langle \ldots \rangle_T$ denotes a thermal average taken over the Gibbs probability distribution:

$$\mathcal{W}(\mathbf{x}) = \frac{1}{Z}\delta(N - \sum_i x_i)\exp[-\beta\mathcal{H}(\mathbf{x})]. \tag{14}$$

We make the replica symmetric ansatz, *i.e.*, we assume that the saddle-point parameters are symmetric under permutations of the replica indices, that is, $\hat{q}^{\gamma\delta} = \hat{q}$, $q^{\gamma\delta} = q$, $\hat{Q}^{\gamma} = \hat{Q}$, $Q^{\gamma} = Q$ and $\hat{R}^{\gamma} = \hat{R}$. Using this procedure the evaluation of equation (9) is straightforward. In order to clarify our results for the replica symmetric average free-energy density it is convenient to introduce the new variables

$$\eta = (\hat{Q} + \hat{q}),$$
$$\tau = \frac{\hat{R}}{\sqrt{2(\hat{Q} + \hat{q})}}$$

and

$$\theta = \frac{\hat{q}}{2(\hat{Q} + \hat{q})},$$

in such way that

$$\begin{aligned} -\beta f = {} & \frac{\eta}{2}[Q - 2\theta(Q - q)] - \beta Q\left(u - \frac{\alpha}{2}\right) + \tau\sqrt{2\eta} \\ & - \frac{\alpha}{2}\ln[\beta(Q - q) + 1] \\ & - \frac{\alpha\beta q}{2[\beta(Q - q) + 1]} + \frac{1}{2}\ln\left(\frac{\pi}{2\eta}\right) \\ & + \int_{-\infty}^{\infty} \mathrm{D}z \ln\left\{\exp[(\tau + z\theta^{1/2})^2]\mathrm{erfc}(\tau + z\theta^{1/2})\right\}, \end{aligned} \tag{15}$$

where

$$Dz = \frac{\mathrm{d}z}{\sqrt{2\pi}}\exp(-z^2/2) \tag{16}$$

is the Gaussian measure. In the zero-temperature limit, the saddle-point equations $\partial f/\partial\eta = 0$, $\partial f/\partial Q = 0$, $\partial f/\partial q = 0$, $\partial f/\partial\theta = 0$ and $\partial f/\partial\tau = 0$ result in

$$\eta = 2u - \alpha + \frac{\alpha}{y + 1}, \tag{17}$$

$$\theta = \frac{\alpha q}{2(y + 1)[(2u - \alpha)(y + 1) + \alpha]}, \tag{18}$$

$$\tau = \sqrt{\frac{\eta}{2}}\left[\frac{1}{\eta} - q + 2\theta y\right], \tag{19}$$

$$\sqrt{2\eta} + \tau\mathrm{erfc}\left(\frac{\tau}{\sqrt{2\theta}}\right) - \frac{2\theta^{1/2}}{\sqrt{2\pi}}\exp\left(-\frac{\tau^2}{2\theta}\right) = 0 \tag{20}$$

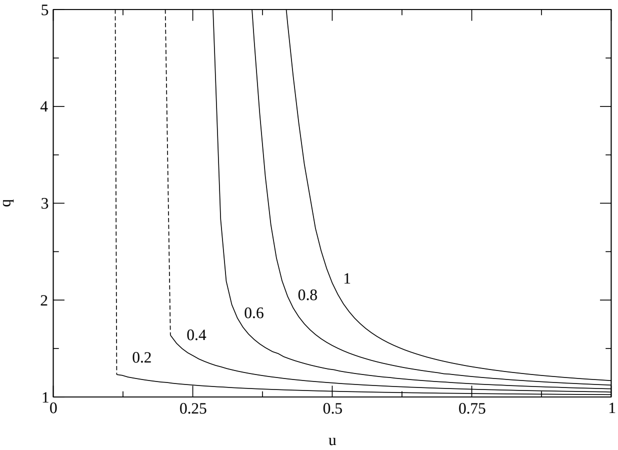

Fig. 1. The order parameter q as a function of the self-interaction u. The lines correspond to $\alpha = 0.2$, 0.4, 0.6, 0.8 and 1 (as indicated in the figure).

and

$$-\eta y + \frac{1}{2}\mathrm{erfc}\left(\frac{\tau}{\sqrt{2\theta}}\right) = 0, \tag{21}$$

where $y = \beta(Q - q) < \infty$. We have taken the limit $T \to 0$ to ensure that only the states that minimize $\mathcal{H}(\mathbf{x})$ contribute to Z.

In the replica-symmetric regime, the order parameter q is defined as

$$q = \left\langle \frac{1}{N}\sum_i \langle x_i \rangle_T^2 \right\rangle. \tag{22}$$

Values of q of the order 1 indicate the coexistence of a macroscopic number of species, *i.e.*, $x \approx 1$ for an extensive number of species, whereas large values of q indicate the dominance of few species. In Figure 1 we present q as a function of the cooperation pressure u for different values of parameter α. For large u, q tends to 1 independently of α, which indicates that the ecosystem is cooperative and so the majority of species survives. In the plot we show that q diverges for $u < \alpha/2$, indicating a strongly competitive regime. For $\alpha < 1/2$, q displays a discontinuity for $u = \alpha/2$. The discontinuity is due to the appearance of another root in one of the saddle-point equations, that provides another value for q that has a larger free-energy density. The results in Figure 1 are clear evidence that the lower the complexity of species composing the ecosystem, the easier it is to get a cooperative ecosystem. (By complexity we mean the number of traits $p = \alpha N$.)

3.1 Stability analysis

To obtain the region where the replica-symmetric solution is stable, we need to calculate the transverse eigenvalues γ_1 and γ_2 [10] of the matrices of the second derivatives of G_1 and G_2 with respect to $q^{\gamma\delta}$ and $\hat{q}^{\gamma\delta}$, respectively, that

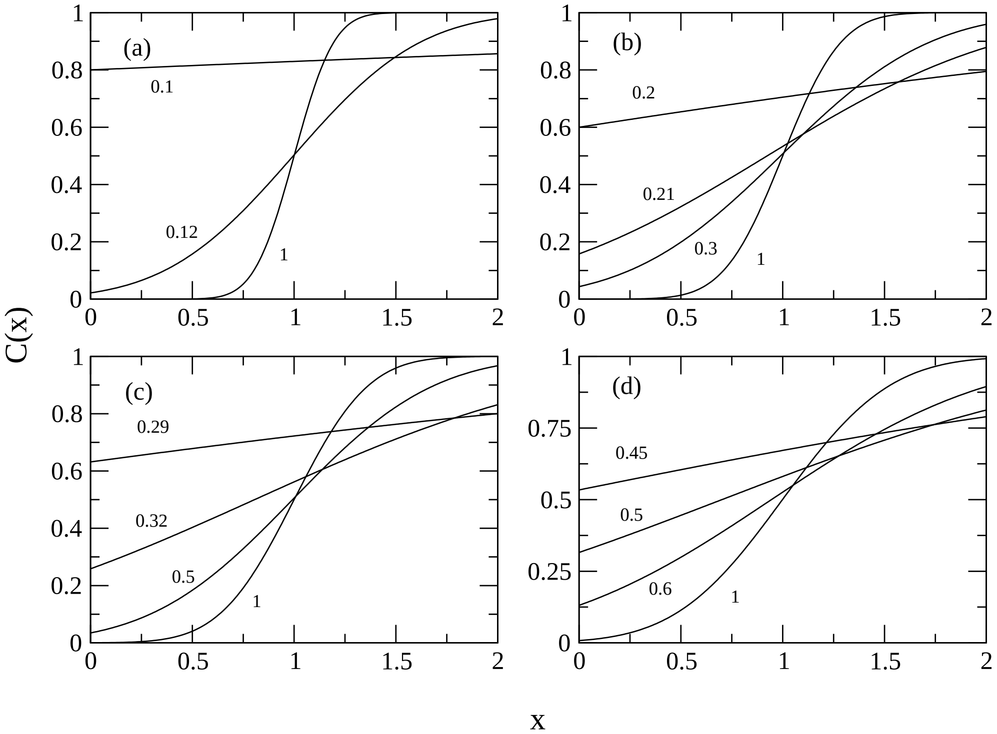

Fig. 2. The cumulative distribution of species concentrations for (a) $\alpha = 0.2$, (b) $\alpha = 0.4$, (c) $\alpha = 0.6$, (d) $\alpha = 1$ and some values of parameter u (as indicated in the figure).

are evaluated at the replica-symmetric saddle-point. The stability condition is given by [9]

$$\alpha\gamma_1\gamma_2 \leq 1. \tag{23}$$

After some algebric manipulations we get

$$\frac{\alpha}{(y+1)^2}\int_{-\infty}^{\infty} Dz(\langle x^2\rangle - \langle x\rangle^2)^2 \leq 1, \tag{24}$$

where

$$\langle x^n\rangle = \frac{\int_0^\infty \mathrm{d}x x^n \exp(-\frac{\eta}{2}x^2 - \sqrt{2\eta}(\tau + \theta^{1/2}z)x)}{\int_0^\infty \mathrm{d}x \exp(-\frac{\eta}{2}x^2 - \sqrt{2\eta}(\tau + \theta^{1/2}z)x)}, \tag{25}$$

so that the final solution is

$$\frac{\alpha}{\eta^2(y+1)^2} \leq 1. \tag{26}$$

Solving numerically equation (26), we have found that the stability condition is always satisfied for u larger than $\alpha/2$.

4 Probability distribution of the concentrations of species

A better understanding about the diversity of species in the ground-state can obtained through the calculation of the probability distribution of the concentrations of species. Thus, the probability that a species has concentration $x_k = x$ is evaluated by

$$\mathcal{P}_k(x) = \lim_{\beta\to\infty}\left\langle \int_0^\infty \prod_i \mathrm{d}x_i \delta(x_k - x)\mathcal{W}(\mathbf{x})\right\rangle, \tag{27}$$

where $\mathcal{W}(\mathbf{x})$ is given by equation (14). As all the species concentrations are equivalent, we consider

$$\mathcal{P}(x) = \mathcal{P}_k(x) = \frac{1}{N}\sum_k \mathcal{P}_k(x). \tag{28}$$

In order to handle a possible singularity in the limit $\beta \to \infty$, we can alternatively consider the cumulative distribution function

$$\mathcal{C}(x) = \int_0^x \mathrm{d}x'\mathcal{P}(x'). \tag{29}$$

Carrying out the calculations within the replica-symmetric framework we obtain

$$\mathcal{C}(x) = 1 - \frac{1}{2}\mathrm{erfc}\left[\frac{\tau}{\sqrt{2\theta}} + \frac{x}{2}\sqrt{\frac{\eta}{\theta}}\right], \tag{30}$$

where τ, θ and η are given by the saddle-point equations (17–21).

In Figure 2 we present the cumulative distribution of the species concentrations for several values of α and u. From the figure, we can notice that a small value of the

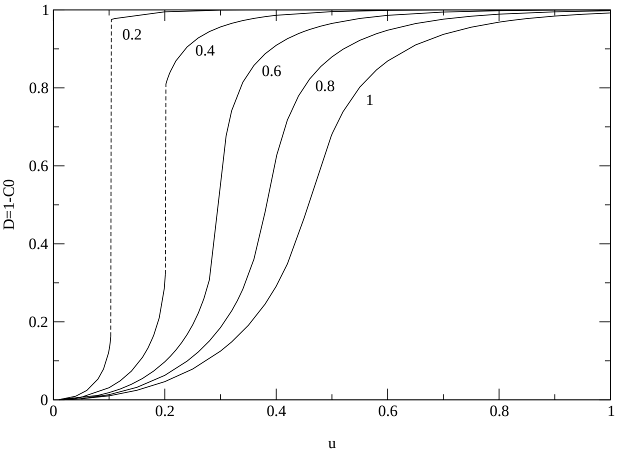

Fig. 3. Species diversity as a function of the self-interaction u. The different curves correspond to $\alpha = 0.2$, 0.4, 0.6, 0.8 e 1 (as indicated in the figure).

cooperation pressure u is necessary in order to attain a regime of cooperation among species in the ecosystem (where the fraction of extinct species $\mathcal{C}(0)$ is equal to zero) when α is not large. As the complexity of the species is increased, a larger u is needed to support the cooperative regime.

In Figure 3 we plot the diversity of species $D = 1-\mathcal{C}(0)$ as a function of the parameter u for several values of α. From the results we can infer that only a few species can coexist when the cooperation pressure u is equal to zero, although an increase in the number of surviving species is observed with the increment of u. For large α the growth in the diversity occurs in a smooth way, whereas for $\alpha < 1/2$ a discontinuity is observed.

5 Concluding remarks

We investigated analytically an ecosystem model at which the species are characterized by an infinite set of p traits, and the interactions between pairs of species are a function of the traits according to a complementarity principle. We used the replica approach to study the average properties of the equilibrium states of the system. The replica-symmetric solution is stable when the self-interaction parameter in the Hamiltonian $(u - \alpha/2) \sum_i x_i^2$ is positive. We also noticed a growth in diversity of species when the cooperation pressure is incremented. This growth is discontinuous for $\alpha < 0.5$, indicating that the diversity increases rapidly in this regime. All our results suggest that the larger the complexity of species, the more difficult it is to find complementary species in the ecosystem. This effect can be circumvented with the introduction of a higher cooperation pressure. Similar behavior has been observed in molecular evolution theory. In the quasispecies model it was observed that there is a maximum value for the complexity of the organism, beyond which the selective information is lost. In order to eliminate the problem other mechanisms such as catalysis have been proposed.

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