

Controlling species richness in spin-glass model ecosystems

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Within the framework of the random replicator model of ecosystems, we use equilibrium statistical mechanics tools to study the effect of manipulating the ecosystem so as to guarantee that a fixed fraction of the surviving species at equilibrium display a predefined set of characters (e.g., characters of economic value). Provided that the intraspecies competition is not too weak, we find that the consequence of such intervention on the ecosystem composition is a significant increase on the number of species that become extinct, and so the impoverishment of the ecosystem.

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I. INTRODUCTION

Experimental studies that manipulate species richness by using synthesized model ecosystems are beginning to unveil how the interactions among species affect the structure of ecosystems (see, e.g., [1,2]). Intensive land use in agriculture may be viewed as one such large scale, though uncontrolled, experiment. In this paper we show how the effects of a similar manipulation can be investigated within the random replicator model framework [3,4]. This is achieved by imposing that a certain fraction of the species that compose the ecosystem at equilibrium exhibit a series of predetermined features (e.g., features of economic value). We then look at the overall effect of this intervention on the structure of the ecosystem.

We assume that the concentration of individuals of species $i=1, \dots, N$ in the ecosystem, described by the real-valued quantity $x_i \in [0, N]$, is governed by the replicator equation [5,6],

$$\frac{dx_i}{dt} = x_i(\mathcal{F}_i - \phi), \quad (1)$$

where $\mathcal{F}_i = -\sum_j J_{ij} x_j$ can be identified with the fitness of species i and ϕ is a Lagrange multiplier that enforces the constraint

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

for all t . Following common practice in taxonomy, we admit that each species is characterized by a set of p phenotypic characters or features, $\mu=1, \dots, p$ [7]. To identify whether species i exhibits or not a given character, say ν , we introduce the binary variables ξ_i^ν such that $\xi_i^\nu=1$ means that species i possesses that character and $\xi_i^\nu=-1$ that it does not [8]. We note that by assuming that the number of characters is extensive, i.e., $p=\alpha N$ with α of order 1, we guarantee that each species is assigned a unique set of characters. In fact, we can easily verify that the probability that two species are assigned the same set of characters vanishes as $2^{-\alpha N} N^2$ in the limit of large N . Since p is the number of features needed to specify the species, it is logical to associate α with the overall complexity of the species that compose the ecosystem and hence with the complexity of the ecosystem itself.

In line with the competitive exclusion principle [9], which asserts that two species living together cannot occupy the same ecological niche, we assume that the intensity of the competition between any two species is proportional to the number of features they share. Hence it is natural to introduce the Hebb rule

$$J_{ij} = \frac{1}{N} \sum_{\mu=1}^p \xi_i^\mu \xi_j^\mu, \quad i \neq j \quad (3)$$

as a prescription for the strength of the interaction between species i and j [8]. Accordingly, $J_{ij} > 0$ must correspond to pairs of competing species whereas $J_{ij} < 0$ to pairs of cooperating species. Equation (3) is the celebrated Hebb rule, extensively studied in the 1980s in the context of attractor neural networks (see, e.g., [10]). As in the neural networks context, from the biological viewpoint the fact that the interspecies coupling J_{ij} is symmetric can be viewed as an utterly unrealistic assumption which, on the other hand, allows a full equilibrium statistical mechanics analysis of the model ecosystem. Relaxation of this assumption, allowing thus the investigation of asymmetric couplings as well, is possible through the use of generating functional techniques. The results obtained for the asymmetric interactions, however, are qualitatively similar to those for the symmetric case [11,12].

In the case of *symmetric* interactions and for zero temperature, the asymptotic regime of Eq. (1) can be fully described by examining the maxima of the fitness functional [3]

$$\mathcal{F}(\{x_i\}) = - \sum_{i,j} J_{ij} x_i x_j \quad (4)$$

subject to constraint (2). As usual, this constraint is taken into account by the addition of an extra term to Eq. (4), $\hat{R} \sum_i x_i$, where \hat{R} is a Lagrange multiplier. In this setting, it can be shown that the only stationary states are fixed points [6]. In addition, we note that in this case the Lagrange multiplier ϕ in Eq. (1) is interpreted as the mean fitness of the ecosystem, i.e., $\phi = \frac{1}{N} \sum_i x_i \mathcal{F}_i$.

Manipulation of the ecosystem composition is achieved by introducing an additional set of constraints

$$m_\nu = \frac{1}{N} \sum_i \xi_i^\nu x_i \quad (5)$$

for $\nu=1, \dots, s$, where s is finite in the thermodynamic limit. This means that the fraction $(1+m_\nu)/2$ of the species that form the ecosystem exhibit character ν . For example, $m_\nu = 1$ represents the extreme situation in which all surviving species must possess character ν . Clearly, $m_\nu \in [-1, 1]$ is the overlap between the N -dimensional character vector $(\xi_1^\nu, \dots, \xi_N^\nu)$ and the equilibrium species concentration (x_1, \dots, x_N) .

As the last ingredient in the definition of the random replicator model we introduce a quadratic damping term that accounts for the self-limitation in the growth of each species, $J_{ii}=u > 0$ for all i . This term prevents the unbounded growth of any single species in the thermodynamic limit $N \rightarrow \infty$, and so we will refer to u as the intraspecies competition parameter.

In what follows we carry out a standard equilibrium statistical mechanics analysis of the ecosystem model defined by the fitness functional (4) and the constraints (2) and (5). This study is feasible provided we assume that the feature variables ξ_i^ν 's are independent random variables.

II. STATISTICAL MECHANICS ANALYSIS

As usual, we introduce the partition function

$$Z = \int_0^\infty \prod_i dx_i \delta\left(N - \sum_i x_i\right) \prod_{\nu=1}^s \delta\left(Nm_\nu - \sum_i \xi_i^\nu x_i\right) \times \exp[\beta\mathcal{F}(\{x_i\})], \quad (6)$$

where $\beta=1/T$ is the inverse temperature. Taking the limit $T \rightarrow 0$ in Eq. (6) ensures that only the states that maximize \mathcal{F} will contribute to Z . Here we focus on the zero-temperature limit so T can be viewed as an auxiliary parameter necessary to carry out the calculations but devoid of any physical meaning. We refer the reader to Refs. [13,14] for a full analysis of the effects of $T > 0$ in the case constraint (5) is relaxed.

Assuming that the ξ_i^μ 's are independent random variables that take on the values ± 1 with equal probability, we must calculate the average free-energy density f defined by

$$-\beta f = \lim_{N \rightarrow \infty} \frac{1}{N} \langle \ln Z \rangle, \quad (7)$$

where the notation $\langle \dots \rangle$ stands for the average over the probability distribution of the quenched random variables ξ_i^μ , $\mu = 1, \dots, p$. The evaluation of this average is carried out through the replica method, which consists of calculating $\langle Z^n \rangle$ for integer n , i.e., $Z^n = \prod_{a=1}^n Z^a$ and then using the identity

$$\langle \ln Z \rangle = \lim_{n \rightarrow 0} \frac{1}{n} \ln \langle Z^n \rangle, \quad (8)$$

in which it is implicit the analytical continuation to $n=0$ [15]. The calculation of Eq. (8) is rather standard (see, e.g., [14,16,17]), except for the fact that the low or condensed

character vectors ξ_i^μ , $\mu=1, \dots, s$, must be treated differently from the high or uncondensed ones ξ_i^μ , $\mu=s+1, \dots, p$. More pointedly, following the same procedure used in the neural networks case [18], we explicitly average out the high character vectors, as well as their overlaps with the equilibrium species concentration, but use the self-averaging property to carry out the average over the low character vectors. Within the replica-symmetric framework we find

$$-\beta f_{rs} = 2q\hat{q} + \hat{R} + \sum_{\nu=1}^s m_\nu(\hat{m}_\nu - \beta m_\nu) - \frac{\alpha\beta q}{1 + 2\beta(Q - q)} + Q[\hat{Q} - \beta(u - \alpha)] - \frac{1}{2} \ln(\hat{Q} + 2\hat{q}) - \frac{\alpha}{2} \ln[1 + 2\beta(Q - q)] + \left\langle \int Dz \ln[e^{\Xi_z^2} \text{erfc}(\Xi_z)] \right\rangle_\xi, \quad (9)$$

where

$$\Xi_z = \frac{\hat{R} + \sum_\nu \hat{m}_\nu \xi^\nu - 2\hat{q}^{1/2}z}{2(\hat{Q} + 2\hat{q})^{1/2}} \quad (10)$$

and we have dropped trivial additive factors. Here $Dz = \exp(-z^2/2) dz / \sqrt{2\pi}$ is the Gaussian measure and the notation $\langle \dots \rangle_\xi$ stands for the average over the statistically independent variables ξ^ν distributed by

$$\prod_{\nu=1}^s \left[\frac{1}{2} \delta(\xi^\nu - 1) + \frac{1}{2} \delta(\xi^\nu + 1) \right]. \quad (11)$$

The saddle-point parameters \hat{R} and \hat{m}_ν enter the calculations as Lagrange multipliers used to enforce constraints (2) and (5), respectively. Similarly, \hat{Q} and \hat{q} are Lagrange multipliers associated to the two physical order parameters of the model,

$$Q = \frac{1}{N} \sum_i \langle \langle x_i^2 \rangle \rangle_T \quad (12)$$

and

$$q = \frac{1}{N} \sum_i \langle \langle x_i \rangle^2 \rangle_T. \quad (13)$$

Here the thermal average is calculated using the replica-symmetry prescription for the Gibbs distribution

$$\mathcal{W}(\{x_i\}) = \delta\left(N - \sum_i x_i\right) \prod_{\nu=1}^s \delta\left(Nm_\nu - \sum_i \xi_i^\nu x_i\right) \times \frac{1}{Z} \exp[\beta\mathcal{F}(\{x_i\})]. \quad (14)$$

The saddle-point parameters q , Q , \hat{R} , \hat{q} , \hat{Q} , and \hat{m}_ν are obtained by solving the $5+s$ coupled nonlinear equations that result from extremizing the free-energy with respect to each of them. The situation is considerably simplified in the zero-temperature limit $\beta \rightarrow \infty$, in which the states that maximize

the fitness functional (4) are singled out. In this limit, it is convenient to introduce the auxiliary parameters, $\Delta = \hat{R}/2\hat{q}^{1/2}$, $\hat{M}_\nu = \hat{m}_\nu/2\hat{q}^{1/2}$, $\lambda = (\hat{Q} + 2\hat{q})/\beta$, $r = \hat{q}/\beta^2$, and $v = 2\beta(Q - q)$. Note that, according to Eqs. (12) and (13), v is proportional to the average variance of the species concentration at equilibrium and so $v > 0$. The saddle-point equations in the zero-temperature limit are then written as

$$v = \frac{1}{\lambda} \left\langle \int_{\Delta'}^{\infty} Dz z(z - \Delta') \right\rangle_{\xi}, \quad (15)$$

$$1 = \frac{r^{1/2}}{\lambda} \left\langle \int_{\Delta'}^{\infty} Dz(z - \Delta') \right\rangle_{\xi}, \quad (16)$$

$$m_\mu = \frac{r^{1/2}}{\lambda} \left\langle \xi^\mu \int_{\Delta'}^{\infty} Dz(z - \Delta') \right\rangle_{\xi}, \quad (17)$$

$$\lambda = u - \frac{\alpha v}{1 + v}, \quad (18)$$

$$Q = \frac{r^{1/2}}{\lambda} \left[r^{1/2} v - \sum_{\nu} m_\nu \hat{M}_\nu - \Delta \right], \quad (19)$$

$$r = \frac{\alpha Q}{(1 + v)^2}, \quad (20)$$

where $\Delta' = \Delta + \sum_{\nu} \hat{M}_\nu \xi^\nu$. We note that by considering m_ν as a saddle-point parameter as well, and so maximizing f_{rs} with respect to it, one gets the additional equation $m_\nu = r^{1/2} \hat{M}_\nu$ which, together with Eq. (17), yields $m_\nu = \hat{M}_\nu = 0$. In this case one recovers the equations for the relaxed case [17], indicating that, in the absence of the constraint (5), half of the species exhibit any given character whereas the other half do not. Because the probability distribution of the binary variables ξ_i^μ is unbiased, the resulting saddle-point equations are invariant to the change $m_\nu \rightarrow -m_\nu$ and so we can consider $m_\nu \in [0, 1]$ without loss of generality.

For completeness, we also calculate the de Almeida-Thouless condition [19] that must be satisfied by the saddle-point parameters in order that the replica-symmetric solution is locally stable. We find (see [20] for details of a similar calculation)

$$\Lambda = \frac{\alpha}{\lambda^2(1 + v)^2} \left\langle \int_{\Delta'}^{\infty} Dz \right\rangle_{\xi} < 1. \quad (21)$$

III. SADDLE-POINT PARAMETERS

The parameter Q has a direct ecological interpretation, namely, it is proportional to the probability that two randomly selected individuals belong to the same species, a measure known as Simpson's index in the ecology literature [21]. Henceforth we will refer to Q as Simpson's index, though, strictly, the correct definition of that index is Q/N . In

addition, we will refer to parameter v as the susceptibility since it measures the fluctuations of the species concentrations around the equilibrium value.

To avoid the undue proliferation of parameters, in this contribution we deal with the symmetric constraint $m_\nu = m$ for $\nu = 1, \dots, s$ only. This means that the fraction of species exhibiting any of the s selected characters is $(1 + m)/2$. As a result we have $\hat{M}_\nu = \hat{M}$ and the relevant random variable becomes $\eta = \sum_{\nu} \xi^\nu$ which takes on the values $-s, -s+2, \dots, s-2, s$ with probability

$$P_\eta = 2^{-s} \binom{s}{\frac{s + \eta}{2}}. \quad (22)$$

It is instructive to consider first the limit $u \rightarrow \infty$ of the saddle-point equations (15)–(20). Since in this limit $\lambda \rightarrow u$ diverges, finite values for the physical order parameters can be obtained provided that $\Delta' \rightarrow -\infty$. As this condition implies that both Δ and \hat{M} diverge as well, it is useful to introduce the new variable $\gamma_0 \equiv \Delta/\hat{M}$ which is given by the solution of the equation

$$sm = \sum_{\eta \geq -\gamma_0} P_\eta(\gamma_0 + \eta) \eta / \sum_{\eta \geq -\gamma_0} P_\eta(\gamma_0 + \eta). \quad (23)$$

In writing this equation we have used the result that $\hat{M} < 0$ for $m > 0$. In fact, because $P_\eta = P_{-\eta}$ the sole effect of changing the sign of m is the change of the sign of \hat{M} as well (note that $\hat{M} = 0$ for $m = 0$) and so \hat{M} changes sign only if m does so. In addition, we have verified numerically that \hat{M} and m have opposite signs. Once γ_0 is known, the quantity $\gamma_1 = -r^{1/2} \hat{M}/\lambda$ is given by

$$\gamma_1 = 1 / \sum_{\eta \geq -\gamma_0} P_\eta(\gamma_0 + \eta). \quad (24)$$

Finally, noting that in this limit $v \rightarrow 1/u \rightarrow 0$ we can write $Q = \gamma_1(\gamma_0 + sm)$ which, as expected, is independent of α . In general, this procedure has to be carried out numerically. However, if $\gamma_0 > s$ then the sums in Eqs. (23) and (24) can be carried out explicitly yielding $\gamma_0 = 1/m$ and $\gamma_1 = m$. Hence $Q = 1 + sm^2$ provided that $sm < 1$, which is always the case for $s = 1$.

The extreme situation $m = 1$ (i.e., only the species i for which $\xi_i^1 = \xi_i^2 = \dots = \xi_i^s = 1$ can survive) admits an analytical solution parametrized by the integer $k = 0, 1, \dots$, namely

$$\gamma_0 = -(1 - 2^{-k})s, \quad s \in \{2^k + 1, \dots, 2^{k+1}\} \quad (25)$$

so that γ_0 is piecewise linear with s . For instance, $\gamma_0 = 0$ for $s = 2$, $\gamma_0 = -s/2$ for $s = 3, 4$, $\gamma_0 = -3s/4$ for $s = 5, \dots, 8$, etc. The result for the Simpson's index is surprisingly simple in this limit, namely, $Q = 2^s$ (see Sec. IV).

In Fig. 1 we illustrate the dependence of the reciprocal of parameter Q on m for different values of s . These results show that the increase of the number of selected species s , which measures the extension of the external intervention on the ecosystem, occasion a significant reduction of the ecosystem diversity.

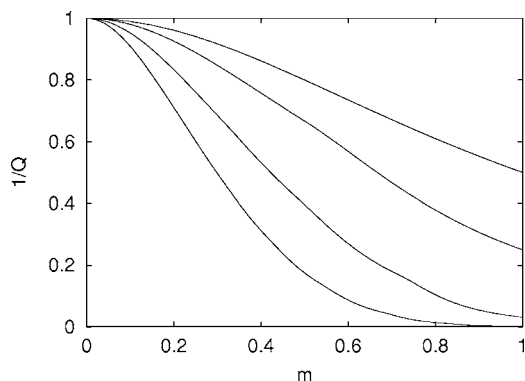


FIG. 1. Reciprocal of Simpson's index as function of m in the limit $u \rightarrow \infty$ for (top to bottom) $s=1, 2, 5,$ and 10 , regardless of the value of α . In this limit we find $v=0$.

We turn now to the general case of finite u . A remarkable fact about the Hebb-like interspecies interactions in the case $m=0$ is the appearance of a discontinuity when the parameter Q is plotted against u or α , as the result of the divergence of v at $u=\alpha$ for $\alpha < 1/2$ [16,17]. Recalling that values of Q close to unity are associated with a rich ecosystem (in the sense that most of the N species coexist) whereas high values of Q are associated with poor ecosystems (a few species dominate the ecosystem) the discontinuity indicates that there are either rich or poor ecosystems: intermediate diversity values are not allowed. The effect of constraining the equilibrium states according to Eq. (5) is summarized in Figs. 2 and 3 that present the numerical results for $s=1$ and $s=5$, respectively. Only the solutions for which $v > 0$ are shown.

The trick to solving the set of saddle-point equations is to consider Δ as a fixed, given parameter and u as unknown. By varying Δ we can find the saddle-point solutions for different values of u . This procedure is effective because all saddle-point parameters can readily be obtained, once Δ is given. Explicitly, to obtain \hat{M} we solve the equation that results from the ratio between Eqs. (17) and (16),

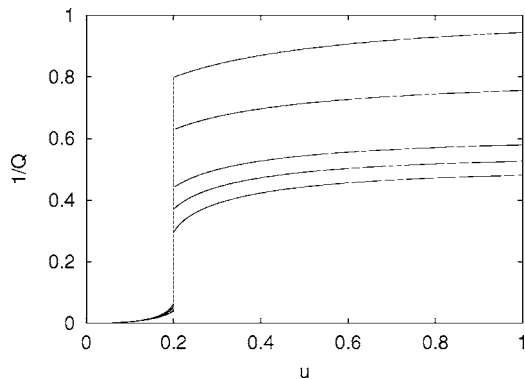


FIG. 2. Reciprocal of Simpson's index as a function of the intraspecies competition parameter u for $s=1, \alpha=0.2$ and (top to bottom for $u > 0.2$ and bottom to top for $u < 0.2$) $m=0, 0.5, 0.8, 0.9,$ and 0.99 .

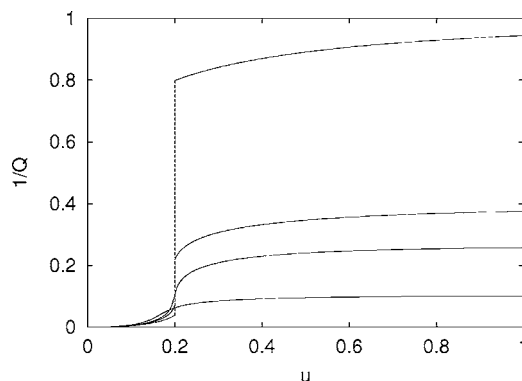


FIG. 3. Reciprocal of Simpson's index as a function of the intraspecies competition parameter u for $s=5, \alpha=0.2$ and (top to bottom at $u=1$) $m=0, 0.5, 0.6,$ and 0.8 . The discontinuity disappears for $m > 0.54$.

$$sm = \frac{\left\langle \eta \int_{\Delta'}^{\infty} Dz(z - \Delta') \right\rangle_{\eta}}{\left\langle \int_{\Delta'}^{\infty} Dz(z - \Delta') \right\rangle_{\eta}}, \quad (26)$$

where $\Delta' = \Delta + \hat{M}\eta$ and the average $\langle \dots \rangle_{\eta}$ is taken with the distribution (22). Once \hat{M} is known, we can calculate Q using Eq. (19) in which $r^{1/2}/\lambda$ is given by Eq. (16) and $r^{1/2}v$ is obtained by taking the ratio of Eqs. (15) and (16), which yields $r^{1/2}v = 1/T(\Delta')$ where

$$T(\Delta') = \frac{\left\langle \int_{\Delta'}^{\infty} Dz(z - \Delta') \right\rangle_{\eta}}{\left\langle \int_{\Delta'}^{\infty} Dz z(z - \Delta') \right\rangle_{\eta}}. \quad (27)$$

The next step is to use Eq. (20) to write

$$v = \frac{1}{(\alpha Q)^{1/2} T(\Delta') - 1} \quad (28)$$

and then to obtain λ via Eq. (15). Finally, the value of u that corresponds to the value of Δ used in this procedure is obtained using Eq. (18).

The first point to be noted in Figs. 2 and 3 is that the discontinuity, when present, always take place at $u=\alpha$, provided $\alpha < 1/2$, regardless of the value of m . In fact, the saddle-point equations admit a solution with diverging susceptibility v provided that λ vanishes so as to keep the product λv finite, as given by Eq. (15). Thus Eq. (18) implies that $u=\alpha$ [17]. The second remarkable fact we learn from these figures is that, at least for $s=5$, the discontinuity may disappear altogether if the value of m is sufficiently large. In fact, a more detailed study, summarized in Fig. 4, indicates that this happens for any $s > 1$. In particular, the curves in this figure are obtained by seeking the value of α for which the denominator in the expression for v , Eq. (28), has no roots.

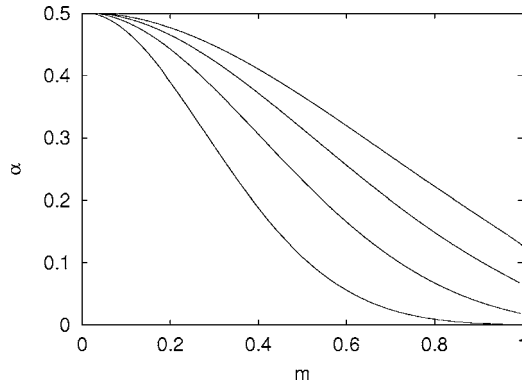


FIG. 4. The value of $\alpha \leq 0.5$ below which the parameter Q exhibits a discontinuity at $\alpha = u$ as a function of m for (top to bottom) $s=2, 3, 5$, and 10 . For $s=1$, the discontinuity is present regardless of the value of m .

A word is in order about the stability of the replica-symmetric solution. In the regime in which there is a discontinuity in Q , only the solutions corresponding to high values of $1/Q$ (upper branch) fulfill condition (21) and so are locally stable. On the other hand, when there is no discontinuity in Simpson's index (e.g., for $\alpha > 1/2$ regardless of s and m) the replica-symmetric solution becomes unstable for values of u slightly smaller than α . This is illustrated in Fig. 5 where the susceptibility v is shown in the nonsingular regime ($\alpha=0.6$, in the case) and the local stability limit is indicated by the dashed curve. Increase of m results in a slight expansion of the region of replica symmetric stability. Since we have verified that, in general, such expansion is very small, we can take $u=\alpha$ as a good guess for the stability boundary in all cases.

IV. ECOSYSTEM STRUCTURE

An important measure used to gain information on the structure of ecosystems is the relative abundance of each species in the community. For instance, classic studies based on samples of insects [22] and plants [23] led to the conclu-

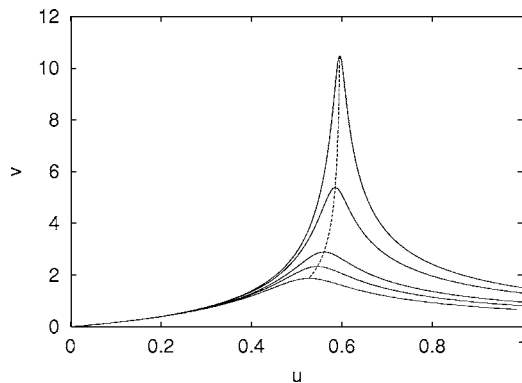


FIG. 5. Susceptibility v as a function of the intraspecies competition parameter u for $s=1$, $\alpha=0.6$ and (top to bottom) $m=0, 0.5, 0.8, 0.9$, and 0.99 . The dashed line indicates the limit of stability of the replica-symmetric solution, which is unstable for small u .

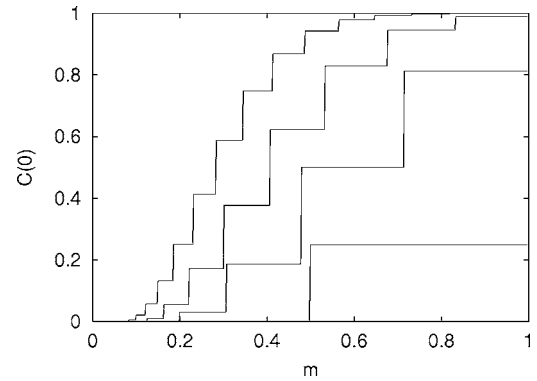


FIG. 6. Fraction of extinct species as a function of m in the limit $u \rightarrow \infty$ for (top to bottom) $s=20, 10, 5$, and 2 . For $sm < 1$ we find $C(0)=0$ and for $m=1$, $C(0)=1-2^{-s}$ (not shown in the figure).

sion that their abundances are distributed geometrically, i.e., most species are relatively rare, whereas a few species are fairly common. In general, however, the log-normal distribution, that describes the situation in which the most numerous category contained species of intermediate abundance, seems more adequate to fit survey data, specially in thoroughly censused communities [24].

To obtain the distribution of abundance in the random replicator model framework we begin by calculating the cumulative distribution that the concentration of a given species, say x_k , assumes a value smaller than x , defined by

$$C_k(x) = \lim_{\beta \rightarrow \infty} \left\langle \int_0^x \prod_j dx_j \Theta(x - x_k) \mathcal{W}(\{x_j\}) \right\rangle, \quad (29)$$

where $\Theta(x) = 1$ if $x \geq 0$ and 0 otherwise, and $\mathcal{W}(\{x_j\})$ is given by Eq. (14). Since all species concentrations are equivalent we can write $C_k(x) = C(x) \forall k$ and evaluate Eq. (29) by adding the field term $h \sum_i \Theta(x - x_i)$ to Eq. (4). Taking the derivatives of the resulting free-energy with respect to h and then the limit $h \rightarrow 0$ yield

$$C(x) = 1 - \frac{1}{2} \left\langle \operatorname{erfc} \left[\frac{\Delta' r^{1/2} + \lambda x}{(2r)^{1/2}} \right] \right\rangle_{\eta}. \quad (30)$$

From the cumulative distribution we can derive the probability density that the abundance of a randomly chosen species takes on the value x , namely,

$$P(x) = \delta(x)C(0) + \frac{dC(x)}{dx}, \quad (31)$$

where the Dirac delta takes care of the singularity at $x=0$.

As before, it is instructive to examine first the limit $u \rightarrow \infty$ in detail. Using the notation of Sec. III we can rewrite Eq. (30) as

$$C(x) = 1 - \sum_{\eta \geq -\gamma_0 + x/\gamma_1} P_{\eta} \quad (32)$$

with P_{η} given by Eq. (22). The fraction of extinct species $C(0)$ can be calculated explicitly for $sm < 1$ and yields $C(0)=0$. The dependence of $C(0)$ on m is shown in Fig. 6. If one counts the single point at $m=1$ as one plateau, then the

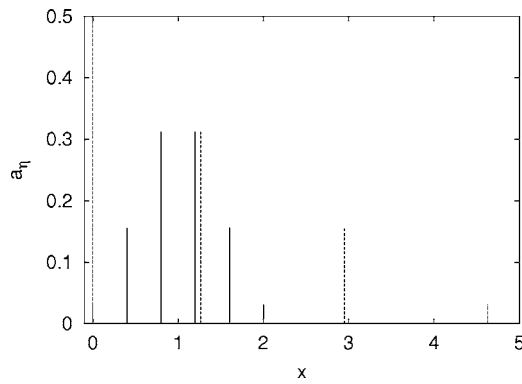


FIG. 7. Amplitudes at the allowed abundance values in the limit $u \rightarrow \infty$ for $s=5$, $m=0.2$ (solid lines) and $m=0.5$ (dashed lines). In both cases, only species characterized by $\eta=1, 3$, and 5 contribute to the ecosystem composition.

number of plateaus for fixed s equals the allowed values of η , namely, $s+1$. Of course, $C(0)=0$ for $m < 1/s$ is considered a plateau as well. From this figure we can see that the distribution of species abundance is given by sums of deltas, $P(x) = C(0)\delta(x) + \sum_{\eta} a_{\eta} \delta(x - x_{\eta})$ with $x_{\eta} = \gamma_1(\gamma_0 + \eta)$ and the sum is restricted to values of η for which $x_{\eta} > 0$. Note that for $m=1$ only $\eta=s$ contributes to the sum in Eq. (32) and so $C(0) = 1 - 2^{-s}$. Furthermore, since $\sum_{\eta} P_{\eta} x_{\eta} = 1$ we find $x_s = 2^s$. Similarly, $Q = \sum_{\eta} P_{\eta} x_{\eta}^2$ implies that $Q = 2^{2s}$ for $m=1$, as pointed out in Sec. III.

The lack of closed expressions for γ_0 and γ_1 precludes an analytical formulation for general s , but for $s=1$ we find

$$P(x) = \frac{1}{2} \delta(x - 1 + m) + \frac{1}{2} \delta(x - 1 - m). \quad (33)$$

Here the first peak is associated to $\eta = \xi^1 = -1$ and so $x_{-1} = 1 - m$ gives the abundance of the species that lack character $\nu=1$, whereas the second peak is associated to the other species type, the abundance of which is $x_1 = 1 + m$. In this case $a_{-1} = a_1 = 1/2$. Figure 7 exhibits the amplitudes a_{η} associated to each x_{η} together with $C(0)$ at $x=0$, for $s=5$. Differently from $C(0)$ (see Fig. 6), the number of impulses is usually less than the possible values of η , due to the restriction in the

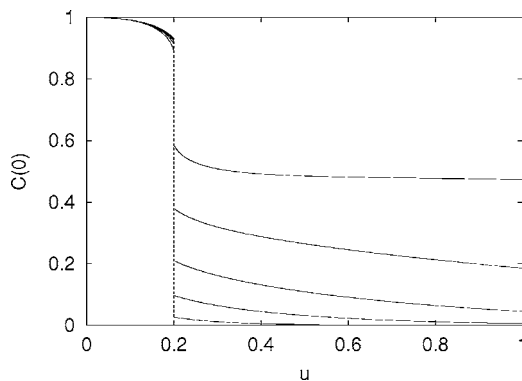


FIG. 8. Fraction of extinct species as a function of the intraspecies competition parameter u for $s=1$, $\alpha=0.2$ and (bottom to top at $u=1$) $m=0, 0.4, 0.6, 0.8$, and 0.99 .

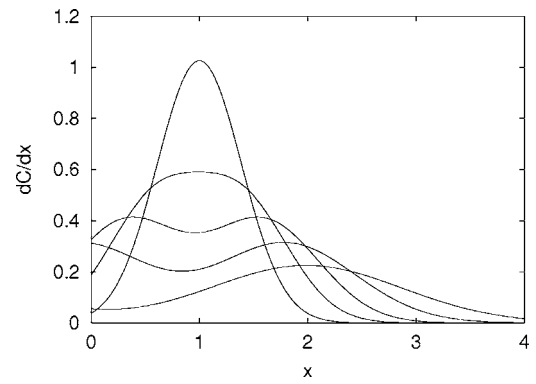


FIG. 9. Finite part of the distribution of abundance for $s=1$, $\alpha=0.2$, $u=0.4$ (top to bottom at $x=1$), $m=0, 0.4, 0.6, 0.8$, and 0.99 .

sum over η mentioned above. The species labeled by η , the abundance of which is given by x_{η} exhibit exactly $(\eta+s)/2$ of the selected s features. Hence the species characterized by $\eta=-s$ are the first ones to go extinct, since for fixed γ_0 and γ_1 we have the sequence of inequalities $x_{-s} < x_{-s+2} < \dots < x_s$. [Note that according to Eq. (24) γ_1 is a positive-defined quantity.] In fact, for the data shown in Fig. 7 only the species displaying 3, 4, and 5 of the selected five features are present in the ecosystem. We stress that the specification of the selected s features solely does not define a species uniquely, since a species is fully identified by the list of the $p = \alpha N$ features. Hence there are an infinity of distinct species characterized by a given value of η .

We turn now to the case of finite u . The fraction of extinct species at the equilibrium regime, given by $C(0)$, is shown in Fig. 8 for $s=1$. Below the threshold value, $u_c = \alpha = 0.2$ for the data exhibited in this figure, the constraint m has little effect on the abundance distribution, but for $u > u_c$ and m close to 1 approximately half of the species go extinct, namely, those species that lack character $\nu=1$, since this is the only way to satisfy simultaneously constraints (2) and (5). The strong correlation between the fraction of surviving species or diversity $1 - C(0)$ (Fig. 8) and the reciprocal of Simpson's index $1/Q$ (Fig. 2) justifies our use of that index as a measure of the richness or diversity of the ecosystem. In fact, for $m=1$ and $u \rightarrow \infty$ both quantities assume the value 2^{-s} .

The finite contributions to the distribution of abundance are shown in Figs. 9 and 10 for $s=1$ and $s=5$, respectively, where we have chosen values of u and α for which the replica-symmetric saddle-point parameters are locally stable. The fact that these distributions become multimodal at intermediate values of m is not a surprise: the smooth peaks observed in these figures are akin to the delta pulses described in the limit $u \rightarrow \infty$. Those pulses are smoothed out by the noise resulting from the random interspecies interactions, which are no longer negligible for finite u . Although in this case we do not have a neat interpretation of the peak locations as the abundance of a certain species type, it is still possible to associate each peak with a given value of η by looking separately at the contribution of each η to the cumulated distribution, Eq. (30). Following this line of action, we have verified that the smooth peaks conform to the pattern described before for the delta pulses.

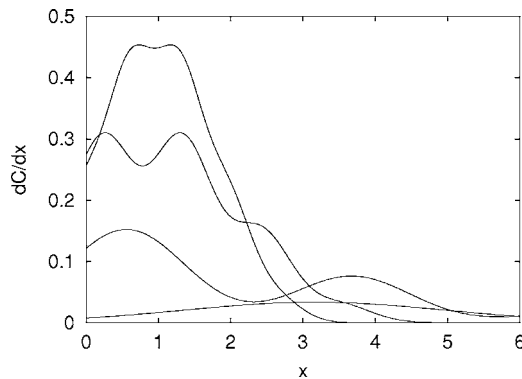


FIG. 10. Finite part of the distribution of abundance for $s=5$, $\alpha=0.1$, $u=0.4$ (top to bottom at $x=1$), $m=0.3, 0.4, 0.6$, and 0.8 .

V. CONCLUSION

The determinant factors to specify the strengths (and signs, as well) of the interspecies interactions in a secluded community are the very features that distinguish a species from the others. For instance, species that pursue similar ways of life must compete with one another for resources — the more similar they are, the fiercer the competition is. This setting can be neatly modeled within the random replicator framework [3] by considering Hebb-like interspecies interactions [8]. Two key elements in that formulation are the identification of species i by a binary string $(\xi_i^1, \xi_i^2, \dots, \xi_i^p)$ where $\xi_i^\mu = 1$ or -1 indicates that species i displays or lacks character μ , and the use of rule (3) to describe the interspecies interactions.

In this contribution we explore the possibility to identify each species unambiguously in order to model human impact on the ecosystem. This is achieved by imposing that a certain fraction of the community at the stationary regime is represented by species with predetermined characteristics [see Eq. (5)], say, characteristics of economic value (monocultures or mixture of few cultures). We find that the average fitness of the constrained ecosystem is lower than that of the unconstrained one. In particular, the optimal composition is that in which only half of the species display any given feature. The effect of such intervention on the ecosystem diversity, measured either by the reciprocal of Simpson's index $1/Q$ or by the fraction of surviving species $1-C(0)$, is quite complex (see, e.g., Figs. 2, 3, and 8). For instance, in the case the intraspecies competition, set by the parameter u , is small (more precisely, $u < \alpha$) the intervention actually helps to increase the diversity, though the increment is rather small. For large u , however, the reduction in diversity due to enforcing the presence of species displaying the selected features can be very pronounced. The practical impossibility to determine *a priori* whether the effect of human intervention would be harmful or not to the species of a generic ecosystem is the reason that the elucidation of the factors that affect diversity

in real ecosystems remains an open issue in the ecology research agenda (see [25] for a review).

An important aspect of the prescription (3) for the interspecies interactions is that it embodies the notion of complementarity among species with different traits. Two species are said to be complementary whenever their coexistence results in an average fitness higher than that obtained if the individual species had grown alone [25]. Hence one expects that by artificially selecting some characteristics to be present in the ecosystem, one inadvertently promotes the presence of the complementary species, the characteristics of which are probably unwelcome. This phenomenon can be observed by looking at the distribution of abundance in the community, defined by Eq. (31). In fact, if a single culture ($s=1$) is enforced then the complementary species is always present as shown in Eq. (33) and Fig. 9. If, however, the community is composed of a few selected cultures ($s > 1$) then totally (or almost so) complementary species can be excluded from the ecosystem (see Figs. 7 and 10).

Since in this contribution we have opted to present the relevant quantities as functions of u for fixed α , a word is in order about the role of the parameter α , which can be associated with the complexity of the species. As in the unconstrained situation, we find that increase of α results in a reduction of diversity, indicating thus that the number of species that can coexist decreases with the complexity of the species [17].

From the perspective of the statistical mechanics of disordered systems—the random replicator is a spin-glass model in which the spin variable is restricted to the hyperplane defined by constraint (2)—we find the interesting result that by increasing the number or the strength of the constraints on the equilibrium state (i.e., by incrementing the values of s or m) the discontinuity of Simpson's index disappears altogether. We note, however, that the more subtle transition, associated to the local instability of the replicator-symmetric saddle-point parameters, is always present and, in particular, that the constraints slightly enlarge the replica symmetric phase.

In summary, we have focused on the effect of manipulating the ecosystem so as to guarantee that a fraction of the surviving species at equilibrium display a selected set of features (e.g., features of economical interest). Within the framework of the random replicator model of ecosystems in which the interspecies interactions are symmetric and the population well mixed, we find that in most cases the consequence of this intervention is the increase of the number of species that become extinct, leading thus to the impoverishment of the ecosystem.

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