Complementarity and diversity in a soluble model ecosystem

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Complementarity among species with different traits is one of the basic processes affecting biodiversity, defined as the number of species in the ecosystem. We present here a soluble model ecosystem in which the species are characterized by binary traits and their pairwise interactions follow a complementarity principle. Manipulation of the species composition, and so the study of its effects on the species diversity, is achieved through the introduction of a bias parameter favoring one of the traits. Using statistical mechanics tools we find explicit expressions for the allowed values of the equilibrium species concentrations in terms of the control parameters of the model.

One of the main interests in the study of model ecosystems is to elucidate the rules governing the assemblage of ecological communities. In particular, understanding the critical role that species composition plays in ecosystem processes can provide useful guidelines to management efforts on behalf of endangered species. Theory has been prominent in the study of long-term effects of species composition on ecosystem functioning, owing mainly to the difficulty to keep controlled experimental conditions in place for a long period (for a recent remarkable exception, see [3]). In these studies, $N$ species are considered to interact in a given community so that their population numbers or biomasses, denoted by $x_1, \ldots, x_N$, are determined by the dynamical equations

$$\frac{dx_i}{dt} = x_i G\left(x_i, \sum_j^N J_{ij} x_j\right)$$

(1)

where $G(\ )$ is a species-independent nonlinear function, such as Ricker dynamics [4], giving the rate of increase of each population and $J_{ij}$ is the interaction coefficient measuring the effect of species $j$ on species $i$ [4,5]. As a rule, the number of species (diversity) $N$ is taken as the control parameter or independent variable and the total biomass (productivity) $\sum_i x_i$, viewed as a measure of the ecosystem stability, as the dynamical variable [4,5,6]. However, especially in long-term studies of large ecosystems this approach is faulty since it does not take into account the dynamics of diversity and the species potential for adaptation to environmental fluctuations [4].

In this contribution we consider an alternative approach in which the diversity is given by the number of surviving species in the ecosystem at equilibrium, being thus a dynamical variable that, ultimately, depends on the nature of the species composing the ecosystem. In particular, we assume that the fraction or concentration of individuals of species $i$ in the ecosystem, $x_i \in [0, \infty)$, is determined by the nonlinear system of equations, so-called replicator equations [7],

$$\frac{dx_i}{dt} = x_i \left(\mathcal{F}_i - \frac{\phi}{N}\right)$$

(2)

where $\mathcal{F}_i = \sum_j J_{ij} x_j$ can be identified with the fitness of species $i$ and the term $\phi = \sum_i x_i \mathcal{F}_i$ ensures that

$$\sum_{i=1}^N x_i = N$$

(3)

for all times. This constraint enforces an effective competition among the species in the ecosystem. We note that by dropping the $\phi$ term in Eq. (2) we recover the classical equation of Lotka-Volterra [4].

In the case of symmetric interactions $J_{ij} = J_{ji}$ the asymptotic regime of Eq. (2) is simply characterized: the dynamics maximizes the Lyapunov function or fitness functional

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

(4)

and so it can be shown that the only stationary states are fixed points [4]. In this case $J_{ij} < 0$ corresponds to pairs of cooperating species whereas $J_{ij} > 0$ to pairs of competing species. The equilibrium regime as well as some aspects of the dynamics can become nontrivial, however, in the case that the functional $\mathcal{F}$ has many local maxima. This occurs when the coupling strengths $J_{ij}$ are quenched random variables taking on positive and negative values, as in the model of random replicators put forward by Diederich and Opper [10] (for further development see [11,12]). The assumption of random interactions is a form of taking into account our lack of knowledge of how the species actually interact. Moreover, it allows the use of tools of the statistical mechanics of disordered systems to fully characterize the equilibrium states, thus making feasible the study of large ecosystems. In contrast, to keep numerical accuracy under control, the traditional approach based on the numerical solution of Eq. (1) is restricted to ecosystems composed of typically $N = 10$ species. We note that in the random replicator framework the productivity $\sum_i x_i$ is constant, while the diversity varies since a fraction of the $N$ species may go extinct due to outcompetition. This phenomenon becomes appreciable, and hence passive of quantitative analysis, for large $N$ only.

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Up to now studies of the random replicator model have considered the strengths of the interactions between species as independent, Gaussian distributed random variables \( \xi_i^\mu, \mu = 1, \ldots, p \), and that the resulting interactions between pairs of species depend on these traits according to a complementarity principle. Specifically, we assume that the traits \( \xi_i^\mu \) are quenched, independent random variables that can take on the values +1 and −1 with probabilities \((1 + a)/2\) and \((1 - a)/2\), respectively. Here \( a \in [0, 1] \) is a bias towards the trait +1, corresponding, e.g., to an economically favored feature of the species. In this sense, the parameter \( a \) may be thought of as a measure of the human impact on the species composition of the ecosystem. In addition, we assume that the coupling strength between species \( i \) and \( j \) is given by the Hebb rule

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

(5)

that was extensively studied in the eighties within the neural networks context \[13, 16\]. Clearly, the larger the number of complementary traits (i.e., \( \xi_i^\mu \xi_j^\mu = -1 \)), the more cooperative the pair of species. Complementarity among species with different traits has been suggested as one of the major mechanisms involved in biodiversity. In that context, the term complementarity subsumes all local deterministic processes which increase the performance of communities above that expected from the performance of individual species grown alone \[8\]. If community performance is measured in terms of the fitness functional \[3\] then the Hebb coupling between species \( \xi_i^\mu \) is clearly well suited to model such processes.

As the final ingredient to define the model, we need to specify the self-interactions \( J_{ii} \). Though for finite \( N \) the constraint \( \sum_i J_{ii} = 0 \) prevents the unbounded growth of any single species, it becomes inefﬁcacious in the thermodynamic limit \( N \to \infty \) and so an additional mechanism to limit growth becomes necessary. The usual procedure is to introduce a competition term between individuals of a same species by setting \( J_{ii} = u > 0 \) for all \( i \) so that \( u \) can be viewed as a global cooperation pressure. In practice, a positive self-interaction is essential to ensure convergence of the numerical methods used to solve the replicator equations \[3\].

The maxima of the functional given in Eq. \[3\] can easily be obtained within the statistical mechanics framework in the limit of inﬁnite \( N \) but ﬁnite \( p \) (see, e.g., \[13\]). We begin by deﬁning the free-energy density \( f \) as

\[
-\beta f = \lim_{N \to \infty} \frac{1}{N} \ln Z
\]  

(6)

where

\[
Z = \int_0^\infty \prod_i dx_i \delta(N - \sum_i x_i) \times \exp \left[ -\frac{\beta}{2N} \sum_\mu \left( \sum_i \xi_i^\mu x_i \right)^2 - \beta u \sum_i x_i^2 \right]
\]

(7)

is the partition function and \( \beta = 1/T \) is the inverse temperature. Taking the limit \( T \to 0 \) in Eq. \( 6 \) ensures that only the states that maximize \( F \) will contribute to \( Z \). After some standard algebraic manipulations \[16\], we find

\[
-\beta f = Q + \frac{m^2}{2\beta} + \ln \left\{ \frac{1}{2} \sqrt{\frac{\pi}{\beta u}} \right\} + \left\langle (Q + m \cdot \xi)^2 \right\rangle_{\beta = 0}
\]

(8)

with the notation \( z \cdot y = \sum_\mu z^\mu y^\mu \) and where we have invoked the self-averaging property of the sums \((1/N) \sum_i g(\xi_i^\mu)\), where \( g \) is any continuous function, to replace them by the species-independent averages \( \left\langle g(\xi^\mu) \right\rangle \). Here \( \langle \ldots \rangle \) stands for the average taken with the probability distribution

\[
\mathcal{P}(\xi) = \prod_\mu \left\{ \frac{1 + a}{2} \delta(\xi^\mu - 1) + \frac{1 - a}{2} \delta(\xi^\mu + 1) \right\}
\]

(9)

The saddle-point parameters \( Q \) and \( m^\mu \) are given by the solutions of the equations \( \partial f/\partial Q = 0 \) and \( \partial f/\partial m^\mu = 0 \). Only \( m^\mu \) has a relevant physical meaning, namely, it is the average overlap between the equilibrium solutions and the trait \( \xi_i^\mu, i = 1, \ldots, N \),

\[
m^\mu = \left\langle \frac{1}{N} \sum_i \xi_i^\mu (x_i)_T \right\rangle
\]

(10)

where \( \langle \ldots \rangle_T \) stands for a thermal average taken with the probability distribution

\[
\mathcal{W}(\{x_i\}) = \frac{1}{Z} \delta(N - \sum_i x_i) \exp [\beta F(\{x_i\})].
\]

(11)

The next step is to take the zero-temperature limit \( \beta \to \infty \). Nonzero solutions for \( Q \) and \( m^\mu \) are found in the regime \( Q + m \cdot \xi < 0 \) only, where the \( p + 1 \) saddle-point equations take on a particularly simple form, whose only solution is the symmetric one \( m^\mu = m \forall \mu \). Explicitly, we find

\[
\hat{m} = \frac{2ua}{2u + 1 - a^2}
\]

(12)

and

\[
\hat{Q} = -2u \left( 1 + \frac{pa^2}{2u + 1 - a^2} \right)
\]

(13)
with the notation $\hat{Q} = Q/\beta$ and $\hat{m} = m/\beta$.

The characterization of the ecosystem through the global parameter $m$ is not very illuminating, and a better understanding can be achieved by looking directly at the values the species concentrations $x_i$ can take on. This can be done, for instance, by calculating explicitly the cumulative distribution that the concentration of a given species, say $x_k$, assumes a value smaller than $x$, defined by

$$C_k(x) = \lim_{\beta \to \infty} \int_0^x \prod_j dx_j \Theta(x-x_k) W\{x_i\}$$

(14)

where $\Theta(x)$ is 1 if $x \geq 0$ and 0 otherwise, and $W\{x_i\}$ is given by Eq. (11). Since all species concentrations are equivalent we can write $C_k(x) = C(x) \forall k$ and evaluate Eq. (14) by adding the field term $h \sum_i \Theta(x-x_i)$ to Eq. (1). Taking the derivatives of the resulting free-energy with respect to $h$ and then the limit $h \to 0$ yield

$$C(x) = \sum_{n=0}^{p} W_n \Theta(x-\zeta_n),$$

(15)

where

$$W_n = \binom{p}{n} \left(\frac{1}{2}\right)^n \left(1 - \frac{1}{2}\right)^{p-n}$$

(16)

and

$$\zeta_n = 1 + \frac{pa}{2u} \left[\frac{a+1}{2} - \frac{2an}{u+1-a^2}\right] \quad n = 0, 1, \ldots, p.$$  \hspace{1cm} (17)

Hence the species concentrations can take on the values $x = \zeta_n$ (provided that $\zeta_n > 0$) only, and the fraction of species with concentration $\zeta_n$ is given by $W_n$. Here the integer variable $n$ yields the total number of traits $+1$ assigned to a given species. The fact that $n$ is the only species feature that determines the equilibrium concentration is consequence of the symmetric solution $m^\mu = m \forall \mu$ of the saddle-point equations. Since $\zeta_0 \geq \zeta_1 \geq \ldots \geq \zeta_p$ the economically more relevant species, i.e., those characterized by the set of traits $\xi^\mu = +1 \forall \mu$, are the first ones to go extinct when, say, the cooperation pressure $u$ decreases. The condition for the coexistence of all species in the ecosystem is then $\zeta_p > 0$ that reduces to

$$p < 1 + \frac{1}{a} + \frac{2u}{a(1-a)}.$$  \hspace{1cm} (18)

We note that the species characterized by $n < p/2$ never die out. A comparison of these analytical results with the numerical solution of Eq. (8) for $N = 2000$ and a single instance of the interaction matrix is presented in Fig. 1 where we show the cumulative distribution $C(x)$ for $p = 5$. For the sake of illustration, the corresponding probability distribution $P(x) = dC/dx$ is also shown in the inset.

The situation of maximum cooperation occurs for $a = 0$ since $\zeta_n = 1 \forall n$ and any particular set of $p$ traits contributes with the same fraction, $2^{-p}$, to the final ecosystem composition. However, this symmetry is broken for $a > 0$. In fact, as the result of the excess of traits $\xi^n = +1$, many different species carry the same or nearly the same set of traits and so their interactions have a strongly competitive character, i.e. $J_{ij} \approx p/N > 0$, explaining thus the depletion of the concentration of species with $n > p/2$. On the other hand, the advantage of species characterized by an excess of traits $\xi^n = -1$ is twofold. First, their relative rarenesses imply that there are few competing species and, second, they have abundance of cooperative partners among the species with $n > p/2$. These two factors explain the dominance, in the sense of occurring at larger concentrations and hence of possessing greater stability, of the species characterized by $n < p/2$. A particularly extreme situation is observed in the limits $u \to 0$ and $a \to 1$, when all species with $n > p/2$ die out. These findings can be given an obvious ecological interpretation, namely, species that are too similar and, consequently, compete for essentially the same resources are prone to extinction. However, the situation is not so simple in the case of a nonzero $u$. For instance, in the limit $a \to 1$ the explosive growth of species with $n < p/2$ can be controlled even by a vanishingly small self-interaction parameter, resulting in the coexistence of all species [see Eq. (18)]. Fig. 2 illustrates the complex dependence of the species diversity $D = 1 - C(0)$ on the control parameters $a$ and $p$ for $u = 0.1$. The results for $u = 0$ are very similar, except in the close neighborhood of $a = 1$ where $D \to 0$, implying that there are a finite number of surviving species only.
FIG. 2: Fraction of surviving species or diversity $D$ as function of the bias parameter $a$ for $u = 0.1$ and $p = 5$ ($\bigcirc$), 10 ($\bigtriangledown$), and 15 ($\triangle$). The solid curves are the theoretical predictions and the symbols are the results of the numerical solution of the replicator equations.

These results indicate that, when complementarity is the sole mechanism determining the species interactions, the assemblage of synthetic ecosystems aiming at the exploitation of some particular traits (as in monocultures, for instance) may, in the long term, be disastrous to the economically relevant species. However, if there is in addition some external global pressure for cooperation, then the best strategy for the long-term survival of those species is to guarantee that they are massively present in the initial assemblage. Even so, the more stable species are always those of less economic value.

Although diversity has been manipulated as an independent variable in most of the numerical studies of model ecosystems as well as in small scale experiments, it is becoming evident that, in large scales, species diversity itself is a dynamical variable that adjusts freely to changes in environmental conditions. The understanding of more complex ecological systems calls then for a more holistic approach. Though relying on the unrealistic, technical assumption of symmetry of the interactions between species, equilibrium statistical mechanics provides an useful (if not the only) analytic framework to tackle this difficult issue. The elusive character of diversity is apparent from our results (see, e.g., Fig. 2) since, despite the simplicity of our model ecosystem, its complex dependence on the control parameters of the model precludes a simple description in terms of a single parameter. This situation is reminiscent of a recent impass in ecology, triggered by the finding of a positive correlation between diversity and productivity in experiments on randomly assembled communities, whereas in nature the most productive ecosystems are those characterized by low species diversity. These antagonistic conclusions may well be due to the attempt to describe productivity solely in terms of diversity, while a complete description would require the knowledge of other, probably uncontrolled, quantities.

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