Statistical mechanics and stability of a model eco-system

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Abstract. We study a model eco-system by means of dynamical techniques from disordered systems theory. The model describes a set of species subject to competitive interactions through a background of resources, which they feed upon. Additionally direct competitive or co-operative interaction between species may occur through a random coupling matrix. We compute the order parameters of the system in a fixed point regime and identify the onset of instability and compute the phase diagram. We focus on the effects of variability of resources, direct interaction between species, co-operation pressure and dilution on the stability and the diversity of the eco-system. It is shown that resources can be exploited optimally only in the absence of co-operation pressure or direct interaction between species.

Keywords: disordered systems (theory), population dynamics (theory), new applications of statistical mechanics
1. Introduction

Models of interacting individuals can be understood as many-body systems of statistical mechanics, and tools developed originally in the context of physics may be employed to address their dynamics and stationary states. This approach has fruitfully been applied to a variety of agent-based models inspired by economics and game theory, see, for example, the recent textbooks [1]–[3]. Attention here focuses on the interplay of co-operation and competition between interacting agents, and on the efficiency of their use of external information and resources. Statistical mechanics here offers a variety of valuable tools to study the global co-operative behaviour of such systems, and to understand their phase structure. In particular, disordered systems theory [4] allows one to address interacting agent models in which interaction matrices are drawn from random ensembles, and to compute typical average quantities for such models. Real-world systems are, of course, not random, but highly correlated. The aim of statistical mechanics approaches is hence often not to study specific instances, but rather the general properties of classes of models as a function of the parameters characterizing the distribution from which couplings are drawn. One may ask, for example, whether quantities such as connectivity, homogeneity or the strength of interaction affect the stability of a given model system. Taking an ensemble average here in a sense corresponds to studying all possible realizations of a given model at the same time, and hence to making statements about effects of model parameters in general, as opposed to analyses of specific real-world instances.
This approach has been used to study, for example, the effects of self-interaction and memory in models of financial trading [1, 2] or to examine how co-operation pressure and order of interactions impact on the stability and trajectories of replicator systems of evolutionary game theory [5]–[7]. In the context of population dynamics models with random interactions were first addressed by May in [8].

In this paper we study a model of a simple food-web composed of species and resources, originally proposed in a more basic form in [9]. The level of the resource consumption by species and its relationship with the stability of the eco-system and the species richness is one of the main issues in ecology [10]. In [9], interaction between species is not through direct interaction (e.g. via prey–predator relations) but exclusively through the use and dependence on resources. If, for example, species $A$ consumes a resource which $B$ feeds upon as well, then this introduces a negative and symmetric interaction between $A$ and $B$. The strength of the negative interaction between $A$ and $B$ is hence regulated by the overlap in their dependence on resources.

Due to the symmetry of interactions the discussion of [9] focuses on a static analysis of this model eco-system. Here we choose a complementary dynamical approach, which allows us to address a broader class of interaction modes. Static studies necessarily rely on the existence of a Lyapunov function, extremized by the trajectories of the eco-system, and are hence limited to systems with symmetric interactions. In the case of an eco-system this is an obvious drawback, as competitive interaction of, for example, prey–predator pairs cannot appropriately be addressed. A direct study of the dynamical equations allows us to extend the analysis to cases of asymmetric interaction matrices, and in particular to discuss the effects of anti-correlation on the behaviour of the system [11, 12]. Asymmetric interaction comes in two ways in the present eco-system. Firstly, we introduce direct interaction between species, in addition to the indirect interaction through the use and dependence on resources. Secondly, we study the effects of possibly asymmetric dilution of the network of interacting species.

The aim of our work here is twofold. Firstly, the study of the present model extends the statistical mechanics analysis of existing replicator models [5]–[7], [11, 12] and relates to studies of Minority Games [1, 2]. Complex phase behaviour and different patterns of ergodicity breaking and instabilities have been identified in such models, with similarities as well as differences between replicator-type models and other systems. One purpose of the present work is thus to contribute to the classification of such models according to the different types of phase transitions they exhibit, and to identify possible universal features.

Secondly, the model system here has a clear-cut ecological interpretation, even though the model may be criticized for not accurately capturing many features of real-world eco-networks. While our approach is a dynamical one, and ultimately results in a stochastic process for a single ‘effective’ species, all disorder in our model is quenched, i.e. the interaction web and coupling strengths are fixed at the beginning, and replicator dynamics are then considered on this fixed network. This approach, on the one hand, makes the model analytically tractable and allows one to reduce the description to a set of a few nonlinear equations describing the relevant order parameters. On the other hand, it constitutes a considerable restriction with respect to real-world eco-systems, in which the web of interaction is, of course, not fixed, but subject to dynamical evolution itself, requiring the study of the dynamics of the network itself in combination with population...
dynamics on the network. Such evolving food-web models have, for example, been presented in [13]–[18]. Related work is also found in [19]–[21]. Results here rely mostly on numerical simulations (see, however, [14] for descriptions in a master equation formalism) and the foodwebs resulting from these models have been compared to real-world data with respect to quantities such as the number of trophic levels, their relative populations and the typical connectivity of species. These models, some of which combine initial Gaussian random score matrices with evolving species networks, clarified the necessary conditions of types of functional responses and dietary choices (specialist/generalist) for producing realistic webs, whose structure agreed with empirical data.

From the technical point of view it is interesting to note that recent stochastic models of complex food-webs [14,15] and the ‘neutral’ model [22] effectively reduce multispecies stochastic process to a ‘one-species’ process of a representative species which is subject to a ‘mean-field’ interaction with the remaining system, and that these models derive reasonable species abundance distributions, in good agreement with real data. In a similar fashion our approach reduces the dynamics of species randomly coupled via quenched interaction to a ‘one-species’ effective process as well. This mapping is fully exact in the thermodynamic limit in the statistical sense. Apart from providing a starting point for more realistic modifications of the present model, our analysis can hence, to a certain degree, be seen as complementary to the approach of [14,15].

This paper is organized as follows: we will first define the model and then briefly discuss the statistical mechanics analysis based on a path-integral approach. We then turn to a stability analysis, and then discuss the effects of resource variation, direct interaction between species, co-operation pressure and dilution in subsequent sections. We summarize our results in the conclusions section and point out lines for potential future research.

2. Model definitions

The model describes an eco-system consisting of $N$ species, labelled by $i = 1, \ldots, N$ and $P = \alpha N$ resources $\mu = 1, \ldots, \alpha N$. $\alpha$ is here a model parameter and is taken not to scale with $N$, i.e. we assume $\alpha = \mathcal{O}(N^0)$. The composition of the eco-system at time $t$ is described by concentrations $x_i(t)$ of species $i = 1, \ldots, N$, which evolve in time according to the following replicator equations [23]:

$$\frac{\dot{x}_i(t)}{x_i(t)} = f_i[x(t), Q(t)] + \nu(t).$$

$f_i$ here denotes the fitness of species $i$ at time $t$ and is frequency-dependent. To be more precise $f_i$ is taken to depend on the composition of the eco-system $x(t) = (x_1(t), \ldots, x_N(t))$ as well as on the abundance of resources $Q(t) = (Q^1(t), \ldots, Q^P(t))$. $\nu(t)$ is a global ‘field’ variable, which is (up to a sign) typically chosen as the mean fitness in order to maintain the overall concentration of species.

We will, in the following, assume that the fitness of species is composed of three contributions $f_i(t) = f_{i,s}[x(t)] + f_{i,r}[Q(t)] + f_{i,c}(x_i(t))$. $f_{i,s}$ denotes a term describing direct species interaction, $f_{i,r}$ refers to interaction due to competition for resources. These two components of the model are illustrated in figure 1 and can be understood as similar to what are referred to as basal and intermediate species, for example, in [16]. $\alpha$ thus controls the relative number of basal species (resources) over intermediate species in our
model. Finally $f_{i,c}$ is an additional contribution describing an external so-called co-operation pressure, driving the eco-system to a state in which all species are present at equal concentrations. We will detail these three contributions to the fitness further in the following.

Following [6] we will choose the direct interaction between species to be characterized by a random coupling, i.e.

$$f_{i,s}[x] = \sum_{j=1}^{N} w_{ij} x_j,$$

(2)

where the matrix elements $\{w_{ij}\}$ are chosen from Gaussian ensembles according to the following distribution:

$$P(w_{ij}, w_{ji}) = \frac{N}{2\pi \sqrt{w^2(1-\Gamma^2)}} \exp \left( -\frac{N(w_{ij}^2 - 2\Gamma w_{ij} w_{ji} + w_{ji}^2)}{2w^2(1-\Gamma^2)} \right)$$

(3)

for any pair $i < j$. The diagonal elements are taken to vanish, $w_{ii} = 0$. Denoting the average over the random couplings by an overbar one thus has

$$\overline{w_{ij}} = 0, \quad \overline{w_{ij}^2} = \frac{w^2}{N}, \quad \overline{w_{ij} w_{ji}} = \Gamma \frac{w^2}{N}.$$  

(4)

$\Gamma$ is a symmetry parameter and takes values $\Gamma \in [-1, 1]$. For $\Gamma = 1$ the interaction between any pair of species $i < j$ is fully symmetric, $w_{ij} = w_{ji}$. For $\Gamma = 0$ $w_{ij}$ and $w_{ji}$ are uncorrelated, and $\Gamma = -1$ corresponds to a prey–predator relation, $w_{ij} = -w_{ji}$. Choosing intermediate values of $\Gamma$ allows one to interpolate smoothly between these regimes. The ecologically most relevant set-up presumably corresponds to negative values of $\Gamma$, describing competitive direct interaction between species, rather than co-operation.

The second contribution $f_{i,r}$ to the fitness of species $i$ describes its propensity to reproduce due to the presence or otherwise of resources. We here follow the lines of [9]. Let us assume that the amount by which species $i \in \{1, \ldots, N\}$ relies on resource $\mu \in \{1, \ldots, P\}$ is described by a coefficient $\xi_i^\mu$, with large $\xi_i^\mu$ signalling a strong dependence

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of \( i \) on \( \mu \). Then we will take \( f_{i,r} [Q] \) to be of the form
\[
f_{i,r} [Q] = \frac{1}{N} \sum_{\mu} \xi_{i}^{\mu} Q^{\mu} (t).
\]
(5)

In turn a large abundance of \( i \) will then deplete the abundance of \( \mu \) so that we write
\[
Q^{\mu} (t) = Q^{\mu} [x(t)] = Q_{0}^{\mu} - \sum_{j} \xi_{j}^{\mu} x_{j} (t).
\]
(6)

\( Q_{0}^{\mu} \) here denotes the abundance of resource \( \mu \) in the absence of species and the second term on the right-hand side corresponds to the consumption of resource \( \mu \) by the different species \( j = 1, \ldots, N \). Recall that a large \( \xi_{j}^{\mu} \) indicates that species \( j \) consumes resource \( \mu \) at a high rate, thus a large concentration \( x_{j} (t) \) (equivalently, a large number of individuals of species \( j \)) adds to the depletion of resource \( \mu \). The availability \( Q^{\mu} (t) \) of resource \( \mu \) thus becomes time-dependent, as the concentrations of species \( \{ x_{j} (t) \} \) evolve in time. In particular it appears interesting to ask the question whether or not the system is able to organize in a state which avoids over- and under-exploitation of resources, i.e. a state in which all \( Q^{\mu} (t) \) remain close to zero asymptotically. We will address this question below.

Following our earlier approach we take the coefficients \( \{ \xi_{i}^{\mu} \} \) to be drawn from a random distribution, specifically we choose them to be independent Gaussian variables, with mean \( q \) and unit variance, i.e.
\[
\xi_{i}^{\mu} = q, \quad \langle (\xi_{i}^{\mu})^{2} \rangle = 1.
\]
(7)

According to the above remarks they describe the interaction between the species layer of the eco-system and the resource layer. While the following analysis focuses mostly on the case of Gaussian \( \{ \xi_{i}^{\mu} \} \) the generating functional theory below and computer simulations show that only the first two moments of the \( \{ \xi_{i}^{\mu} \} \) are relevant, so that more general distributions can be addressed as well with the methods used here. To complete the definition of \( f_{i,r} \), it remains to specify the \( \{ Q_{0}^{\mu} \} \). Following [9] we write
\[
Q_{0}^{\mu} = P + \sigma \sqrt{P} \xi^{\mu}
\]
(8)

with \( \{ \xi^{\mu} \}_{\mu=1,\ldots,P} \) independent standard Gaussian variables. The model parameter \( \sigma \) thus controls the variability of resources. The scaling with \( P = \alpha N \) of the \( \{ Q_{0}^{\mu} \} \) is chosen to guarantee a well defined thermodynamic limit, with which the theoretical analysis will eventually be concerned.

Finally, we will study the effects of co-operation pressure on the eco-system. This variable acts to suppress the growth of individual species and is incorporated by a contribution
\[
f_{i,c} (x_{i}) = -2ux_{i}
\]
(9)

to the fitness of species \( i \) [6, 24]. In an ecological setting \( u \) takes mostly positive values denoting intra-species competition (but see also a comment on potential settings with negative \( u \) below). For \( u \to \infty \) the eco-system is found in a state of perfect co-operation and maximal diversity (with all species surviving and having equal concentrations). As we will confirm later, a reduction of \( u \) leads to a smaller number of surviving species, and hence a reduced diversity. In order to obtain a complete overview of the phase behaviour of the model, we extend the analysis to negative values of \( u \) as well.
The definition of the dynamics (1) is completed by stating the choice of \( \nu(t) \) we will make in the following. In the analysis of the statics of the model it was found that only states with the normalization \( N^{-1} \sum_i x_i = \alpha/q \) contribute to the thermodynamics of the system \([9]\). Accordingly, we also restrict the dynamics to such configurations, and choose initial conditions and the subsequent Lagrange parameters \( \{ \nu(t) \} \) such that the constraint
\[
\frac{1}{N} \sum_i x_i(t) = \frac{\alpha}{q}
\] (10)
is fulfilled at all times. This amounts to the choice
\[
\nu(t) = -\left(\frac{q}{\alpha}\right) \left(\frac{1}{N} \sum_i x_i(t)\right) f_i[x(t), Q(t)].
\]

To conclude the presentation of the model let us briefly point out some of its obvious limitations. Firstly, due to the Gaussian choices of the \( \{ \xi^\mu_i \} \) and of the \( \{ Q^\mu_0 \} \) negative values of these quantities might statistically occur (in the cases of the abundances \( Q^\mu_0 \) this is, however, suppressed in the thermodynamic limit due to the scaling with \( N \) in (8)). Secondly, the replicator dynamics (1) do not guarantee that all \( Q^\mu(t) \) remain positive at all times. These drawbacks are consequences of the solubility of the model, as models with non-Gaussian disorder at the same scaling with \( N \) or additional constraints on the resource abundances are difficult to treat analytically. We would however like to note that with our choice of parameters (e.g. \( q = 1 \)) most of the \( \{ \xi^\mu_i \} \) are indeed positive. The model is furthermore invariant under simultaneous shifts of the means of all \( \{ Q^\mu_0, \xi^\mu_i \} \) so that their averages can be chosen sufficiently high as to minimize the amount of negative couplings.

3. Generating functional and effective species process

3.1. Effective macroscopic theory and fixed point ansatz

The model lends itself nicely to the study by the tools of disordered systems theory. For fully symmetric couplings \( \Gamma = 1 \) one identifies
\[
\mathcal{H} = \frac{1}{2N} \sum_{\mu} Q^\mu(t)^2 - \frac{1}{2} \sum_{i \neq j} w_{ij} x_i(t) x_j(t) + u \sum_i x_i(t)^2
\] (11)
as a Lyapunov function, minimized by the replicator dynamics (1). Thus the stationary state of the model can, in this case, be obtained by purely static considerations based on replica theory. For general symmetry \( \Gamma \) no such Lyapunov function can be found and the analysis needs to deal directly with the microscopic dynamics. The method of choice is here based on generating functionals, originally proposed in the context of random replicators in [6] and recently used in [11,12]. The analysis focuses on the dynamic partition function
\[
Z[\Psi] = \left\langle \exp \left( i \int dt \sum_i x_i(t) \Psi_i(t) \right) \right\rangle
\] (12)
where the average \( \left\langle \langle \cdot \rangle \right\rangle \) extends over all trajectories of the system permitted by the equations of motion. \( \Psi \) is a source field introduced to generate dynamical correlation functions and \( Z[\Psi] \) is hence the Fourier transform of the probability measure on the space...
of paths generated by the replicator equations. $Z[\Psi]$ can then efficiently be averaged over the disorder and evaluated by the method of steepest descents in the thermodynamic limit $N \to \infty$. We will not enter into the detailed mathematics here, but will only report the final outcome\(^4\). One finds a description in terms of effective single-species trajectories, described by the following multiplicative Gaussian stochastic process:

$$\dot{x}(t) = x(t) \left( \int_{t_0}^{t} dt' R(t, t') x(t') - \eta(t) + \nu(t) \right).$$

($t_0$ denotes the time at which the dynamics is started). The key components are the retarded interaction kernel

$$R(t, t') = -2u \delta(t - t') - \Gamma w^2 G(t, t') - \alpha (\mathbb{1} - G)^{-1}(t, t')$$

and the coloured Gaussian noise \(\{\eta(t)\}\) which exhibits temporal correlations of the form

$$\langle \eta(t) \eta(t') \rangle_* = w^2 C(t, t') + \alpha \left[ (\mathbb{1} - G)^{-1}(\alpha \sigma^2 E + C)(\mathbb{1} - G^T)^{-1} \right] (t, t').$$

The matrices $C$ and $G$ in (14) and (15) are the correlation and response functions of the system, respectively, and are to be determined self-consistently as

$$C(t, t') = \langle x(t)x(t') \rangle_* , \quad G(t, t') = -\left\langle \frac{\delta x(t)}{\delta \nu(t')} \right\rangle_* ,$$

where $\langle \cdot \rangle_*$ denotes an average over trajectories of the effective stochastic process (13), i.e. over realizations of the noise $\{\eta(t)\}$. $E$ is the matrix with all entries equal to one, $E(t, t') = 1$ for all $t, t'$.

The analysis proceeds by making a fixed point ansatz $x(t) = x, \eta(t) = \eta, \nu(t) = \nu$ in the effective process, leading to

$$C(t, t') \equiv Q.$$  

Furthermore we assume time-translation invariance of the response, i.e. $G(t, t') = G(t-t')$, and define the integrated response as

$$\chi = \int dt G(t),$$

which we require to be finite for further analysis. This restricts the ansatz to the ergodic regime of the system, i.e. to model parameters for which the assumed fixed point is independent of initial conditions. The following self-consistent equations of the persistent order parameters $\{Q, \chi, \nu\}$ can then be derived along the lines of [6, 11, 12]:

$$\frac{\alpha}{q \sqrt{\lambda}} \left( 2u + w^2 \Gamma \chi + \frac{\alpha}{1 - \chi} \right) = \int_{-\infty}^{\Delta} Dz (\Delta - z),$$

$$\frac{Q}{\chi} \left( 2u + w^2 \Gamma \chi + \frac{\alpha}{1 - \chi} \right)^2 = \int_{-\infty}^{\Delta} Dz (\Delta - z)^2,$$

$$- \left( 2u + w^2 \Gamma \chi + \frac{\alpha}{1 - \chi} \right) \chi = \int_{-\infty}^{\Delta} Dz.$$ \hspace{1cm} (21)

Here $Dz = (1/\sqrt{2\pi}) e^{-z^2/2} dz$ denotes the standard Gaussian measure and one has $\lambda = w^2 Q + \alpha (\alpha \sigma^2 + Q)/(1 - \chi)^2$ and $\Delta = \nu / \sqrt{\lambda}$. We note that $\phi = \int_{-\infty}^{\Delta} Dz = \frac{1}{2} (1 + \text{erf}(\Delta / \sqrt{2}))$ describes the fraction of surviving species.

\(^4\) Imposing the above normalization (10) ensures that no super-extensive terms are found in the generating functional analysis and that the usual saddle-point integration can be carried out in the thermodynamic limit.
3.2. Key observables

We will study in the following the behaviour of the system as a function of the different model parameters and in particular focus on the effects of the different components in the set-up of the eco-system. The above theory allows us to compute the behaviour of the model in the stable fixed-point regime exactly in the thermodynamic limit, and to carry out a linear stability analysis to identify the onset of instability as described below. Theoretical results will be compared to observations in computer experiments based on a numerical integration of the replicator equations (1). We here use the scheme of [7], effectively corresponding to a first-order integrator with dynamical time step. In addition to the above-mentioned fraction of surviving species \( \phi \), we will study the diversity index \( D = \frac{\alpha^2}{(q^2Q)} \), closely related to what is known as Simpson’s diversity index in ecology [25]. Note that if the species concentrations were normalized to one the sum \( \sum_i x_i^2 \) (i.e. the analogue of \( Q = N^{-1} \sum_i x_i^2 \)) would indicate the probability that two randomly chosen individuals belong to the same species. We will also focus on the effectiveness of the use of resources. To this end one defines

\[
H = \frac{1}{N^2} \sum_{\mu} \langle (Q^\mu(t))^2 \rangle
\]

with \( \langle \cdot \rangle \) a time average in the stationary state. Note that \( \langle Q^\mu(t) \rangle = O(N^{1/2}) \), so that \( H \) is of order one in the thermodynamic limit. \( H \) denotes the efficiency with which the species make use of the resources present in the system. If \( H = 0 \) then \( \langle Q^\mu(t) \rangle \neq 0 \) for all \( \mu \), i.e. all resources are optimally exploited. If, however, \( H > 0 \), then the use of a fraction of resources (those with \( \langle Q^\mu(t) \rangle \neq 0 \)) is unbalanced. Our analytical theory allows us to compute \( H \) from the saddle-point equations, and one finds

\[
H = \frac{\alpha \sigma^2 + Q}{2(1 - \chi)^2}
\]

as in [9].

3.3. Stability analysis and phase transitions

The above ansatz of a stable ergodic regime breaks down when either fixed points become numerous or suppressed in the thermodynamic limit. In the first case the system has a large number of (possibly marginally stable) attractors, and initial conditions determine which of these is realized. Hence ergodicity is broken. In the second case the system would not evolve into any fixed point at all at long times.

The breakdown of the fixed point regime can be identified by means of linear stability analysis on the level of the effective process. Details of similar calculations can be found in [6, 11]. For the present model one finds that the system runs into a unique stable fixed point if

\[
w^2\chi^2 + \alpha \frac{\chi^2}{(1 - \chi)^2} < \phi,
\]

and that it becomes unstable when this condition is violated.

Our above fixed-point ansatz also implies the assumption that the integrated response \( \chi \) be finite. A singularity in \( \chi \) would hence signal the breakdown of the ergodic theory.
and the onset of memory effects, in the sense that perturbations in the stationary state do not decay, but remain permanent [2]. Simultaneously, a divergence of $\chi$ necessarily implies $H = 0$ (see equation (23)), and hence a transition to a phase in which resources are optimally exploited. Since the right-hand side $\phi$ (the fraction of surviving species) of equation (21) is bounded ($\phi \in [0,1]$), we find that a divergence of $\chi$ can occur only if $u = 0$ and $w = 0$. Thus we expect no phase with optimal resource exploitation whenever co-operation pressure or direct species interaction are present. Finally we note that (21) implies $\phi = \alpha$ if $|\chi| \to \infty$ in a model system with $u = w = 0$. Thus, the instability condition (24) is violated whenever $\chi$ diverges.

4. Effects of resource variability

We now first examine the effects of the variability of the resources. To this end, we set the strength of the direct species interaction $w$ and the co-operation pressure $u$ to zero in this section, and focus on the behaviour of the model as a function of $\sigma$. This control parameter $\sigma$ measures the fluctuations of $Q_{\mu}^0$ (see equation (8)), i.e. the degree to which the different resources $\mu = 1, \ldots, \alpha N$ vary in their bare abundances $Q_{\mu}^0$ in the absence of species. For simplicity we keep $q = 1$ throughout this section. This system is the model studied in [9] by static methods. A phase transition was found, marked by a divergence of the static susceptibility in a replica symmetric ansatz. We here reproduce this transition from a dynamical calculation and present the results of this section mainly for completeness and to set the scene for the subsequent parts of the paper.

Figure 2 shows the phase diagram obtained by solving the three equations (19), (20) and (21). The transition point $\alpha_c = \alpha_c(\sigma)$ is identified as the point where the integrated response $\chi$ diverges. To obtain an interpretation of this transition in terms of the ergodicity properties of the system, we run two copies $\{x(t)\}$ and $\{x'(t)\}$ of the system with the same realization of the disorder, but starting from different random initial conditions, and measure the distance $d^2 = \langle N^{-1} \sum_i (x_i(t) - x_i'(t))^2 \rangle_t$, between two stationary states of the system. Thus if $d^2 = 0$ initial conditions play no role, while for $d^2 > 0$ the system is sensitive to the starting point. Although numerical measurements of $d^2$ can exhibit finite-size effects, simulations shown in figure 3 are consistent with an ergodic phase above $\alpha_c$, and with a phase in which the system is sensitive to initial conditions below $\alpha_c$. In this second phase the system is still found to evolve into a fixed point, but stationary points of the dynamics become numerous, and which one of these is reached asymptotically is determined by initial conditions, similar to the behaviour of other replicator systems [5–7]. Figure 4 shows that this ergodic non-ergodic transition coincides with a transition between a resource-efficient phase at $\alpha < \alpha_c$ ($H = 0$) and an inefficient phase ($H > 0$) in the phase at $\alpha > \alpha_c$.

In figure 5 we report on the diversity of the eco-system as a function of the resource variability. One finds that the diversity of the ecosystem is large at a large number of resources per species, and that the ecosystem becomes less diverse as the number of resources is reduced. The figures also confirm that the behaviour of $D = \alpha^2/(q^2 Q)$ is similar to the one of the fraction of surviving species $\phi$, hence verifying the role of $D$ as a measure of the diversity of the eco-system. In the following sections we will hence focus on $\phi$. As anticipated in the introduction, results do not depend on the specific shape of the distribution of the $\{\xi_i^n\}$, as only their first and second moments enter in the derivation of
the effective dynamics. We have explicitly confirmed this in simulations, which show that measurements of $H$ and $D$ of systems in which the $\{\xi^\mu\}$ follow flat, exponential, bimodal and power-law distributions with suitable first and second moments fall precisely on the lines obtained from the theory in figures 4 and 5.

The left panel of figure 5 furthermore confirms that $\phi = \alpha$ at the transition with diverging susceptibility $\chi$. Similar transitions in static contexts can be identified by the divergence of the static susceptibility in a replica symmetric approach [9]. The occurrence of this transition has a geometrical interpretation similar to what is know in the context, for example, of Minority Games [26, 27, 1, 2]. In the absence of co-operation pressure and direct species interaction, the fitness $f_i$ in expression (1) is of the form $f_i[Q] = N^{-1} \sum_\mu Q^\mu(t)\xi^\mu_i$, i.e. a linear combination of the $PN$-dimensional vectors $\xi^\mu = (\xi^\mu_1, \ldots, \xi^\mu_N)$. The dynamics of the system thus can only wash out perturbations within the space spanned by the $\alpha N$ vectors $\xi^\mu$, $\mu = 1, \ldots, \alpha N$. Disregarding the $(1-\phi)N$ extinct species, the underlying dynamical system has $\phi N$ effective degrees of freedom. Extinct species are typically stably extinct with respect to perturbations, see also [6]. The space of all potential external perturbations is hence $\phi N$-dimensional. Thus, if $\alpha < \phi$ some of those perturbations cannot be removed by the dynamics, and ergodicity breaking occurs.

The existence of a phase with $H = 0$ at $\alpha < \alpha_c$ can be interpreted similarly. In the absence of direct interaction and co-operation pressure one has $\mathcal{H}$ and $H$ coincide up to pre-factors, and the dynamics minimizes this Lyapunov function. Attaining the absolute minimum $H = 0$ implies $\langle Q^\mu(t)\rangle_t = 0$ for all $\mu$ via (22). This constitutes a system of $\alpha N$
Figure 3. Reduced distance $d^2/Q$ versus $\alpha$ for the model without direct species interaction and co-operation pressure ($w = 0$, $u = 0$, $q = 1$). Symbols show results from simulations for $N > 200$ species, run for $>10\,000$ discretization steps and averaged over at least 20 samples of random resource consumption $\{\xi_i\}$. Vertical dashed lines mark the location of the phase transition as predicted by the theory.

constraints. With $\phi N$ effective degrees of freedom available, these conditions can be met if $\alpha < \phi$, but not above the transition point defined by $\phi(\alpha_c) = \alpha_c$.

5. Effects of direct species interaction

Animals have not only the resource competition but also have the direct species interaction, like prey–predator, co-operation, competition and so on. In this section we study the effects of direct interaction between species, as controlled by the model parameter $w$. In order to focus on the impact of this model parameter we set $u = 0$ throughout this section. We also limit the discussion to the case $q = 1$.

In figure 6 we depict the phase behaviour of the system as direct species interaction is introduced. As predicted by the theory we find that the integrated response $\chi$ is finite in the case $w > 0$ for all tested values of the model parameters. The transition lines in figure 6 hence mark an instability at which $H$ remains positive. They are obtained from equation (24). The figure demonstrates that the phase diagram is indeed affected by the direct interaction between species and by the symmetry of the couplings $\{w_{ij}\}$. The left panel shows that even a relatively moderate direct interaction of strength $w = 0.1$ can have a significant effect: symmetric ($\Gamma = 1$) and asymmetric ($\Gamma = 0$) interactions reduce the stable area while antisymmetric ($\Gamma = -1$) interaction expands the stable region, compared with the case without direct interaction ($w = 0$) shown in figure 2. This is confirmed in
the right panel of figure 6: For symmetric and uncorrelated interaction $\alpha_c$ increases with increasing $w$ so that direct interaction tends to make the system increasingly less stable. For negatively correlated interaction ($\Gamma = -1$) on the other hand, $\alpha_c$ is a decreasing function of $w$, indicating that prey–predator-type interactions stabilize the eco-system. One might speculate that, for that reason, food-webs with this type of interaction may be more likely to be observed in nature than others. For $\Gamma = -1$ we also find $\alpha_c$ approaches zero for large values of $w$, indicating that there is no unstable region in the limit of $w \to \infty$, which is consistent with marginally stable dynamics in the antisymmetric random replicator model without resource competition [28].

The left panel of figure 7 shows that the efficiency of resource exploitation is reduced as direct species interaction is introduced, and is consistent with the predicted absence of a phase in which $H = 0$. The effect is stronger for correlated couplings than for negatively correlated ones. The effects of the direct couplings on the diversity of the eco-system is shown in the right panel of figure 7. One observes relatively little effect for the case of antisymmetric couplings, but a strong reduction of diversity as uncorrelated or positively correlated couplings are introduced. Crucially we here find that $H$ and $\phi$ are smooth functions of $w$ as long as $\alpha > \alpha_c(w = 0)$. In particular no singularities are observed as $w \to 0$. This is different in the case $\alpha = 0.2 < \alpha_c(w = 0) \approx 0.27$, as shown in the insets of figure 7. Here $H \to 0$ as $w \to 0$ and the integrated response diverges. Simulations at finite $N$ reveal non-monotonic behaviour of $\phi$ at $w = 0^+$. While we cannot fully rule out finite-size effects similar discontinuities of order parameters have been found in the context of so-called grand canonical Minority Games [1,2]. The apparent discontinuity of

\[ H \text{ versus } \alpha \text{ for the model without direct species interaction (} w = 0, q = 1 \text{). Curves are for } \sigma = 2, 1, 0 \text{ from top to bottom. The solid lines are from the theory, symbols from simulations (} N = 300, 50 \text{ samples, run for } 20,000 \text{ steps). } H \text{ vanishes below } \alpha_c. \]
6. Effects of co-operation pressure

We now turn to the effects of the co-operation pressure $u$ on the behaviour of the model. We again limit the discussion to the case $\sigma = q = 1$, and consider the system both with and without direct species interaction.

6.1. No direct species interaction

The phase behaviour of the system at $w = 0$ is depicted as a function of the co-operation pressure in figure 8. For completeness we extend the discussion to positive and negative values of the co-operation pressure $u$, although only $u > 0$ carries specific ecological meaning (plants, however, can grow without predation, which might be modelled by a positive self-interaction, corresponding to a negative co-operation pressure in the present model). Most interestingly the phase with optimal exploitation of resources is limited to the interval $u = 0, \alpha \in [0, 0.27]$ on the $u = 0$ axis. In particular, as mentioned above, any positive or negative amount of co-operation pressure removes the phase with $H = 0$. Furthermore as observed in figure 8, the eco-system is fully stable at all $\alpha$ for any positive co-operation pressure, even for infinitesimally small $u > 0$. For $\alpha \gtrsim 0.27$ an unstable phase can only be found at $u < u_c(\alpha) < 0$. Figure 9 confirms that $H > 0$ throughout this phase. As expected $\phi$ grows monotonically with $u$, the co-operation pressure $u$ acts

\[ \phi \]
as a force driving the system into the interior of the simplex (10). For low or negative values of \( u \), on the other hand, the fraction of surviving species is low. Our simulations seem to indicate that \( \phi \) is continuous as \( u \downarrow 0 \) for \( \alpha > \alpha_c(u = 0) \), but that a discontinuity may be present at lower values of \( \alpha \). This is similar to the behaviour of \( \phi \) at low \( \alpha \) as \( w \downarrow 0 \) discussed above (see inset of figure 7). As shown in the right panel of figure 9 \( \phi \) attains values close to zero for \( \alpha = 0.2 \) and \( u < 0 \), whereas the fraction of surviving species is clearly positive at positive \( u \). While our simulations are potentially prone to finite-size effects, the data presented is consistent with a first-order phase transition. Simulations furthermore indicate that \( \phi \) might actually vanish at small enough \( \alpha \) and negative co-operation pressure, indicating the possible existence of a phase in which only a sub-extensive number of species survives. Such behaviour has previously been reported for the case of higher-order interaction in [11]. Due to the limited relevance of negative co-operation pressure we have, however, not conducted a more detailed analysis of these observations and can at this stage not fully confirm the existence of such a phase in this system of two-body interactions.

6.2. With direct species interaction

The phase structure of the model with co-operation pressure and direct species interaction is shown in figure 10. Stable phases are found at large positive co-operation pressures and large relative numbers of resources, and either a reduction of \( u \) or \( \alpha \) can induce instability. In line with earlier observations anti-symmetry in the direct species interactions tends to stabilize the eco-system, at full anti-correlation a stable fixed-point regime is found for

\[ \sigma = 1, q = 1, u = 0. \]

Figure 6. Effect of direct species interactions. Left: phase diagram in the \((\sigma, \alpha)\) plane \((w = 0.1, q = 1, u = 0)\). The curves are obtained from equation (24) and are shown for \( \Gamma = 1, 0, -1 \) from top to bottom. The system is stable above the respective curves and unstable below. Right: phase diagram in the \((w, \alpha)\) plane. \( \sigma = 1, q = 1 \) and \( u = 0 \). Curves are for \( \Gamma = 1, 0, -1 \) from top to bottom. The system is stable above the respective curves.
any $u > 0$ at any $\alpha$, whereas unstable regimes can be found for $\Gamma > -1$ even at positive co-operation pressure. The left panel of figure 11 finally shows that $H$ remains positive throughout all tested parameter ranges if $w > 0$. The right panel demonstrates that again $\phi$ is an increasing function of the co-operation pressure $u$. In contrast with the system at $w = 0$ no discontinuities in the order parameters are observed, as the transition with diverging integrated response is absent.

7. Effects of dilution

Animals, of course, do not have the all-to-all interaction. We now turn to a discussion of the effects of diluting the interaction web between species. We restrict the discussion to the case without direct species interaction and without co-operation pressure, i.e. we consider only $u = w = 0$. We furthermore follow the philosophy of introducing dilution in the context of neural networks [29] and in random replicator models [12], and assume that only a fraction $c \in (0, 1]$ of interaction links between species is present. If an interaction between species $i$ and $j$ is present, then we take it to be determined by their respective use of resources, following [9]. More specifically, we write

$$\dot{x}_i(t) = \frac{1}{N} \sum_{\mu=1}^{\alpha N} \xi_{i\mu}^\mu Q_i^\mu(t) + \nu(t)$$

(25)

where

$$Q_i^\mu(t) = Q_0^\mu - \sum_{j=1}^{N} \frac{\xi_{ij}^\mu}{c} x_j(t)$$

(26)
Figure 8. Phase diagram for the model with co-operation pressure \((w = 0, q = \sigma = 1)\).

Figure 9. Effects of co-operation pressure: efficiency of resource exploitation \(H\) (left) and fraction of surviving species \(\phi\) (right) versus co-operation pressure \(u\) \((w = 0, q = \sigma = 1)\). Solid lines are from the theory in the stable phase, for \(\alpha = 1, 1.5\) continued as dashed lines into the unstable phases with finite integrated response. Symbols are from simulations (circles correspond to \(\alpha = 0.2\), squares to \(\alpha = 1\), diamonds to \(\alpha = 1.5\)) with \(N = 300\), run for 20 000 iteration steps, averaged over 50 samples. Markers for \(\alpha = 0.2\) have been connected as a guide to the eye.
**Figure 10.** Phase diagram for the model with species interaction ($w = 1$) and co-operation pressure. Resource variation is set to $\sigma = 1$. Curves show the onset of instability for $\Gamma = 1, 0, -1$ from top to bottom, with stable phases to the top right, unstable ones to the lower left.

**Figure 11.** Effects of co-operation pressure: efficiency of resource exploitation $H$ (left) and fraction of surviving species $\phi$ (right) versus co-operation pressure $u$ for model with direct species interaction ($w = \alpha = q = \sigma = 1$). Solid lines are from the theory in the stable phase, continued as dashed lines into the unstable phases. Symbols are from simulations, circles correspond to $\Gamma = 1$, squares to $\Gamma = 0$, diamonds to $\Gamma = -1$ (simulations are performed for $N = 200$, run for 10 000 iteration steps, averaged over 20 samples of the disorder).
is the amount of resource $\mu$ available to species $i$ at time $t$. The coefficients $c_{ij}$ denote the dilution of the interactions and take values 0 and 1, indicating a particular link to be absent or present, respectively. An absent link could, for example, correspond to a geographic separation between species. The $c_{ij}$ are here taken to be random, and we choose any $c_{ij}$ to be equal to one with probability $c$, and equal to 0 with probability $1-c$. Consequently we have

$$c = \langle c_{ij} \rangle_c = \langle c_{ji} \rangle_c$$

(27)

for any pair $i < j$, where $\langle \ldots \rangle_c$ denotes an average over realizations of the dilution. Note that $\langle c_{ij}^2 \rangle_c = c$. Correlations in the interaction network are then introduced by the requirement that

$$\langle c_{ij} c_{ji} \rangle_c - c^2 = \gamma c(1-c)$$

(28)

with $\gamma \in [0,1]$. $\gamma = 1$ corresponds to an undirected symmetric network of interactions with $c_{ij} = c_{ji}$ for all $i < j$. For $\gamma = 0$ $c_{ij}$ and $c_{ji}$ are uncorrelated, and the links in the interaction web are hence directed ones. Ecologically realistic cases presumably correspond to $\gamma \approx 1$, for completeness we extend the statistical mechanics analysis of the dilute model to general values $\gamma \in [0,1]$. Finally, we note that, following the conventions in the literature, we write the number of resources as $P = \alpha c N$ in this section, and that we take self-interactions to be present for all species, i.e. we have $c_{ii} = 1$ for all $i = 1, \ldots, N$. We also note that we use $Q_0^\mu = \sigma \sqrt{P} \xi_\mu$ and $\xi_i^\mu = 0$ along with the normalization $N^{-1} \sum_i x_i(t) = \alpha c$ in this section$^5$.

The analysis of the dilute model is straightforward and can be performed along the lines of [29,30,12]. The effective process is

$$\dot{x}(t) = x(t) \left( -\alpha(1-c)x(t') - \alpha \int_{t_0}^t dt' \left[ c(\mathbb{I} - G)^{-1} + \gamma(1-c)G \right] (t,t')x(t') - \eta(t) + \nu(t) \right)$$

(29)

where

$$\langle \eta(t) \eta(t') \rangle = \alpha \left[ c(\mathbb{I} - G)^{-1}(\alpha c^2 E + C)(\mathbb{I} - G^T)^{-1} + (1-c)C \right] (t,t')$$

(30)

and with all other definitions as in the fully connected model.

The resulting phase diagram is depicted in figure 12. As shown, correlated dilution (roughly $\gamma \geq 0.5$) increases the numerical value of $\alpha_c$, and hence reduces the stable regime of the system compared with the fully connected model. At largely uncorrelated dilution $\gamma \leq 0.5$ the location of the phase transition $\alpha_c$ shows only a weak dependence on the degree of dilution $c$. This behaviour is also reflected in figure 13, where we focus on the system at $\alpha = 1.5$ and depict the fraction of surviving species as a function of the connectivity $c$ at different values of the symmetry parameter $\gamma$. For $\gamma$ smaller than roughly one-half, diluting the network of species does not seem to affect the stationary

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$^5$ The modification to the statistics of the $\{Q_0^\mu, \xi_i^\mu\}$ is necessary to guarantee a well-defined thermodynamic limit. While in the fully connected model all terms of order higher than $N^0$ drop out in the dynamical action due to the overall normalization of species concentrations; this would no longer be the case in the dilute model. If the statistics of the $\{Q_0^\mu, \xi_i^\mu\}$ were not modified, $N$ different normalization constraints would be required, due to different local interaction ‘neighbourhoods’ of species. The model specifications used in this section make sure that such terms do not appear.
Figure 12. Phase diagram for the dilute model ($\sigma = 1$). The curves show the transition lines below which fixed points become unstable. $\gamma = 1, 0.75, 0.5, 0.25, 0$ from top to bottom. No divergence of the susceptibility $\chi$ is observed for $c < 1$. At $c = 1$ one reproduces the transition of the model of [9], $\alpha_c(c = 1) \approx 0.27$.

state significantly. The phase transition is absent and the system always reaches a unique stable fixed point at this value of $\alpha$, irrespective of $c$. Uncorrelated dilution furthermore has only little effect on the diversity whereas as highly correlated interaction network can affect the eco-system significantly and reduces the number of survivors. This is in line with our earlier observations on the effect of direct species interaction at different degrees of symmetry, see figure 11.

8. Concluding remarks and outlook

In summary we have used tools from disordered systems theory to study a stylized model of a simple eco-system, composed of a set of species competing for an amount of limited resources, and which at the same time are subject to direct inter-species competition.

The dynamical system of corresponding replicator equations has been addressed by path integral techniques, allowing us in particular to study cases of asymmetric interaction between species (corresponding to prey–predator relations), where there is no Lyapunov function governing the dynamics, and where static approaches are hence inapplicable.

We find that this simple model eco-system displays a rich spectrum of features and interesting phase behaviour separating stable from unstable regimes. Our main findings can be summarized as follows:

(i) in the absence of direct species interaction and co-operation pressure the fully connected model displays a transition between a phase in which initial conditions
Figure 13. Effects of dilution: fraction of surviving species $\phi$ versus $c$ for dilute model at $\alpha = 1.5 \ (\sigma = 1)$. $\gamma = 0, 0.5, 1$ from top to bottom. Solid lines are from theory in the stable phase and have been continued as dashed lines into the unstable phase (where the theory can no longer be expected to be accurate). Symbols are from simulations ($N = 300$, run for 40 000 time steps, averages over at least ten samples are taken; for small values of $c$ simulations may exhibit finite-size effects; also equilibration effects and sample-to-sample fluctuations cannot fully be excluded). The inset shows $d^2/Q$ versus $c$ obtained from simulations for the same model parameters and demonstrates the presence of a transition for $\gamma = 1$ (circles). For $\gamma = 0, 0.5 \ d^2/Q \approx 0$ in line with the theory which for those values of the symmetry parameter predicts the system to be stable for all $c$.

The observed ergodicity breaking are irrelevant and a non-ergodic phase. This transition is also marked by a change of the efficiency of resource exploitation. In the unstable phase resources are used optimally, while this is not the case in the stable phase.

(ii) The introduction of either direct species interaction, co-operation pressure or dilution alters the type of transition observed, in particular the fully efficient phase is removed. One still finds a phase boundary separating a stable ergodic fixed point regime from a non-ergodic phase.

(iii) For symmetric couplings the non-ergodic phase is marked by an exponential number of marginally stable fixed points, see also [6, 7], and initial conditions determine which of these is reached in the long run leading to the observed ergodicity breaking. At asymmetric or partially asymmetric coupling (induced by either direct interaction or dilution) no fixed point is reached in the unstable phase. Instead the trajectories of the system remain volatile and potentially chaotic.
(iv) We observe a general tendency of increased stability when asymmetric (or anti-symmetric) interaction is introduced. This is the case both for direct species interaction and dilution. While the range of stability is then increased, no significant effects on the diversity of the eco-system are found.

(v) The introduction of symmetric interaction or dilution can reduce the stability of the system significantly and at the same time also lead to a reduced diversity of its stationary population structure.

(vi) In the absence of direct species interaction the effects of co-operation pressure can be drastic, and in particular the system is stable at any even infinitesimal amount of co-operation pressure. At small (relative) numbers of resources over species order parameters can display discontinuities as the co-operation pressure tends to zero.

The model studied in the present paper and its phase behaviour are furthermore interesting from the statistical mechanics point of view. As detailed above the transition between a resource-efficient and an inefficient phase in the model without direct species interaction or co-operation pressure has a geometrical interpretation previously identified, for example, in the context of the dynamics of the Minority Game [26, 27]. This geometrical picture breaks down as soon as direct interaction or co-operation pressure are introduced, hence the absence of a transition at diverging integrated response and of the fully efficient phase. The present model may hence serve as a starting point for attempts to fully classify interacting agent models according to the presence or absence of phases with optimal resource exploitation. A close relation to the presence or otherwise of replica symmetry breaking and to the geometry of the manifold of stationary states is here to be expected.

Extensions of the present model might include adding a third or further trophic levels, temporally fluctuating resource availability (e.g. along the lines of [27]) or the introduction of further heterogeneity of the species. It is likely that this will alter the phase diagram and might affect the stability or otherwise of the eco-system. Furthermore the computation of species abundance distributions (SAD), as introduced by Fisher et al [31] and Preston [32], might be an interesting issue for future work. SAD have been measured and compared to log-normal and log-series distributions known in ecology, for example in the model of [14]. The work of Tokita [33] demonstrates that random replicator models can yield SAD similar to left-skewed log-normal distributions. Given the presence of a phase transition in the model discussed here it would be particularly interesting to study finite systems near the transition, resulting in potential non-Gaussian features and fat-tailed abundance distributions (see [1, 2] and references therein for similar critical fluctuations in Minority Game models near their phase transitions). In order to address the resulting topological structure and distribution of coupling strengths it might also be interesting to study the food web resulting from the present model in more detail. In particular, as seen above, some species die out asymptotically, inducing a reduced coupling matrix restricted to survivors only. While species cannot change their foraging strategies and no new links between species can be created in our model, this extinction dynamics might lead to non-trivial, potentially correlated effective interaction strengths distributions among survivors at stationarity. In [34] a dominance of prey–predator pairs in the set of surviving species has, for example, been identified in the context of replicator systems with quenched Gaussian interactions.
Furthermore, it would be interesting to extend the analysis of the dilute model to more realistic finite-connectivity cases on complex networks [35]. So far we have only addressed dilute Erdős–Reyni type networks with an extensive number of connections per node. Complex networks with scale-free degree distribution [35, 36] and the small-world property [37] or other structures might here be of more biological relevance [14, 15, 18], in an approach to approximate dynamically evolved networks by static quenched ones. Extension to such sparse networks might require us to study cases with only a finite number of interactions per species. This is challenging as the resulting effective dynamical theories do not close on the level of two-time order parameters. Still it would be interesting to examine the effects of network topology and degree sequence on the stability or otherwise of the model eco-system, as a first step potentially relying on numerical simulations or on replica approaches and the cavity method [38] in order to study the statics of eco-systems with symmetric couplings.

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