Systems of random linear equations and the phase transition in MacArthur’s resource-competition model

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Abstract – Complex ecosystems generally consist of a large number of different species utilizing a large number of different resources. Several of their features cannot be captured by models comprising just a few species and resources. Recently, Tikhonov and Monasson have shown that a high-dimensional version of MacArthur’s resource competition model exhibits a phase transition from a “vulnerable” to a “shielded” phase in which the species collectively protect themselves against an inhomogeneous resource influx from the outside. Here we point out that this transition is more general and may be traced back to the existence of non-negative solutions to large systems of random linear equations. Employing Farkas’ Lemma we map this problem to the properties of a fractional volume in high dimensions which we determine using methods from the statistical mechanics of disordered systems.

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Introduction. – Ecosystems—from rainforests to the human gut—can harbor a surprisingly large number of different species [1–3]. These species in general compete for a limited number of resources and possibly prey on each other. Inspired by this observation researchers from various fields examine the role biodiversity plays in complex ecosystems and how their community structure is shaped. However, mathematical studies of model ecosystems were mostly performed for systems with only a few species and resources [4–6]. Results obtained for small settings do not straightforwardly generalize to large systems characterized by collective phenomena and emergent properties [7,8]. Starting with the pioneering work of May [9] such phenomena are increasingly addressed by studying large models with random parameters. This is a sensible approach if self-averaging properties of the system may be identified that only depend on the features of the underlying distributions and not on the individual realization of the randomness. Methods from the statistical mechanics of disordered systems then provide useful tools for a quantitative characterization of typical properties of the system [10–13].

Along these lines, Tikhonov and Monasson [10,14] recently investigated a high-dimensional version of MacArthur’s consumer-resource model [4]. In this model, different species compete for a number of resources which are supplied by fixed influxes from the environment. An increasing population size of a species leads to a lower resource availability and consequentially to a reduced growth rate, creating a negative feedback loop. Even though the interactions between the species are purely competitive Tikhonov and Monasson found a transition into a collective phase at large potential diversity, i.e., when the number of available species in the regional pool sufficiently exceeds the number of resources. In this phase, all resources are equally well available and the number of surviving species is equal to the number of resources, saturating the upper bound set by the competitive exclusion principle [15]. Moreover, by performing a stability analysis Altieri and Franz [16] revealed that the collective phase exhibits marginally stable behavior.

In [10] the phase transition was examined by constructing a Lyapunov function for the population dynamics and a subsequent replica calculation characterizing its extremum. In the present letter we show that the transition is more general and may be derived without reference to the actual dynamics of the model. We first point out a connection between stationary states of MacArthur’s model and the space of non-negative solutions to large systems of random linear equations. By the Farkas lemma this
The resource availabilities $h_i$ derive from the resource influxes $R_i$ and are decreasing functions of the total demand $T_i = \sum_{\mu} \sigma_{\mu i} n_{\mu}$ of resource $i$. Different models of resource supply differ in the form of these depletion functions $h_i(T_i)$. We require that if influx and total demand balance for every resource the dynamics (1) should be in a stationary state which according to (2) corresponds to $h_i = 1$ for all $i$. The dependence of the resource availabilities on the total demand is hence given by

$$h_i(T_i) = 1 - f_i(T_i), \quad (3)$$

where the functions $f_i$ are monotonically increasing functions of their argument and satisfy $f_i(R_i) = 0$. We do not need any further specification of the depletion functions in our analysis.

In line with previous investigations [9,10,17] it is assumed that the model parameters $\sigma_{\mu i}$ and $R_i$ are independent random variables. More specifically, $\sigma_{\mu i}$ is taken to be one with probability $p$ and zero with probability $1 - p$. Small values of $p$ therefore describe populations with many specialists whereas large $p$ favours universalists. The $R_i$ are taken to be of the form $R_i = 1 + \delta R_i$ where the fluctuations $\delta R_i$ are Gaussian random variables with zero mean and variance $r^2/N$. The scaled variance $r^2$ remains $O(1)$ for $N \to \infty$ and characterizes as a second central parameter of the model the heterogeneity of resource influxes to the system.

For linearized depletion functions (3) it was shown in [10] that the system possesses two different phases. For small potential diversity, $\alpha \leq \alpha_c$, the system is in the vulnerable or V-phase. Here the inhomogeneity of resource influxes $R_i$ penetrates down to the level of the resource availabilities $h_i$ and the number of surviving species is less than $N$. In contrast, in the shielded or S-phase at large potential diversity $\alpha$, all resource availabilities $h_i$ are equal to one despite the differences in the external influxes $R_i$. In this phase the species form a kind of collective field and shield each other from the external inhomogeneities. At the same time the number of surviving species attains its maximum value $N$.

In their calculation Tikhonov and Monasson construct a convex Lyapunov function $F(n)$ which is bounded from above and increases on every trajectory. They show that the stationary states of the system lie on the boundary of the so-called unsustainable region in the space of resource availabilities

$$U = \bigcap_{\mu=1}^S \{ h \ | \ \sigma_{\mu i} \cdot h < \chi_\mu \}. \quad (4)$$

A partition function of the system is then defined by

$$Z = \int_U \prod_i d h_i e^{\beta \tilde{F}(h)}, \quad (5)$$

where the integration is performed over the unsustainable region and $\tilde{F}(h)$ is the Legendre transform of $F(n)$. In the
limits $\beta, N \to \infty$ the expectation value $\frac{1}{\beta N} \log Z$ is determined by application of the replica trick, thereby characterizing the stationary states and determining the critical line of the phase transition. In the following we present a different approach to the transition which does not make use of the Lyapunov function.

Relation to systems of linear equations. – The phase transition observed in the resource-competition model can be related to a problem in linear algebra. Let us denote by $\hat{\sigma}$ the matrix $\sigma_{\mu i}$ of metabolic strategies, by $n \in \mathbb{R}^{\alpha N}$ the vector of species abundancies, and by $R \in \mathbb{R}^N$ the vector of resource influxes. The central point is that the S-phase is characterized by $h_i = 1$ for all resources $i$. By (3) this implies $T_i = R_i$ for all $i$ and using the definition of $T_i$ it translates to

$$\hat{\sigma}^T n = R. \quad (6)$$

We therefore expect that the system is in the S-phase if these inhomogeneous linear equations possess a non-negative solution $n$, $n_i \geq 0$ and that it is in the V-phase if no such solution exists. Figure 2 tests this assumption on the basis of numerical simulations. Shown is the fraction of random realizations of eq. (6) for which a non-negative solution was found by application of a least squares solver$^2$. It is clearly seen that the solution space of eq. (6) is separated into a phase in which typically no solution exists and a phase in which a solution can always be found. The dashed line marks the phase transition derived in [10]. A similar behavior is found for other values of $p$.

Fig. 2. Average fraction of realizations of eq. (6) which possess a non-negative solution $n$. The solution space clearly separates into a part with typically no such solution (lower right) and a phase in which such a solution typically exists. The dashed line is the critical line determined in [10] and also given by eq. (13) below. The system size is $N = 300$, $p = 0.5$, and each data point was averaged over 50 realizations.

The observed transition becomes sharper when the systems gets larger as shown by the finite-size analysis of fig. 3. As can be seen the steepness of the transition increases with increasing system size $N$ and the extrapolated values of $\alpha_c$ converge to the analytical result given by eq. (13).

Analytical determination of the critical line. – The question whether the linear system (6) for large $N$ typically possesses a non-negative solution $n_i$ can be analyzed analytically. To this end we first employ Farkas’ Lemma [18] that stipulates that for given $\hat{\sigma}$ and $R$ either (6) has a non-negative solution or there is a vector $y \in \mathbb{R}^N$ such that

$$\hat{\sigma} y \geq 0 \quad \text{and} \quad R \cdot y < 0. \quad (7)$$

The intuitive meaning of this theorem is simple: the linear combinations of the row vectors $\sigma_{\mu i}$ of $\hat{\sigma}$ with non-negative coefficients form what is called the non-negative cone of these vectors. If $R$ lies within this cone, there is a non-negative solution to eq. (6); if not, there must be a hyperplane (with normal vector $y$) separating the cone from $R$.

The dual problem defined by (7) is rather similar to the storage problem in the theory of feedforward neural networks [19] and can be addressed by similar means. We define the fractional volume of vectors $y$ that fulfill eq. (7)

$$\Omega(\hat{\sigma}, R) := \frac{\int_{-\infty}^{\infty} \prod_i dy_i \delta(\sum_i y_i^2 - N) \mathbf{1}(y; \hat{\sigma}, R)}{\int_{-\infty}^{\infty} \prod_i dy_i \delta(\sum_i y_i^2 - N)}, \quad (8)$$

with the indicator function

$$\mathbf{1}(y; \hat{\sigma}, R) := \prod_{\mu=1}^{\alpha N} \Theta\left(\frac{1}{\sqrt{N}} \sum_{i} \sigma_{\mu i} y_i \right) \Theta\left(-\frac{1}{\sqrt{N}} \sum_{i} R_i y_i \right). \quad (9)$$

$^2$We used the solver nnls of the scipy.optimize package in Python.
The spherical constraint $\sum_i y_i^2 = N$ is introduced to lift the trivial degeneracy of solutions $y \rightarrow \lambda y$ for any positive $\lambda$. If $\Omega(\sigma, R)$ is zero there are no solutions to (7) and correspondingly there is a non-negative solution to (6). Complementary, if $\Omega(\sigma, R)$ is larger than zero, there are vectors $y$ fulfilling (7) and therefore no non-negative solution to (6) exists. The transition occurs when $\Omega(\sigma, R)$ shrinks to zero.

Due to the product structure of $\Omega$ the entropy $\frac{1}{\beta} \log \Omega$ is expected to be self-averaging with respect to $\sigma$ and $R$. We may hence characterize the typical situation in a large system by considering the average entropy

$$S(\alpha, p, r^2) := \langle \log \Omega \rangle_{\sigma, R}.$$  \hspace{1cm} (10)

With the help of the replica trick [20] and using standard techniques [19] this entropy may be expressed as a saddle-point integral over order parameters (see SM)

$$m^a = \frac{1}{\sqrt{N}} \sum_i y_i^a \quad \text{and} \quad q^{ab} = \frac{1}{N} \sum_i y_i^a y_i^b.$$  \hspace{1cm} (11)

Within the replica-symmetric ansatz we find

$$S(\alpha, p, r^2) = \text{extr} \left[ \frac{1}{2} \log(1-q) + \frac{q}{2(1-q)} - \frac{\kappa^2(1-p)}{2mp^2(1-q)} \right] + \alpha \int Dt \log \left( \frac{\sqrt{q}t - \kappa}{\sqrt{1-q}} \right),$$  \hspace{1cm} (12)

where the extremum is over $\kappa$ and $q$ and the abbreviations $Dt := dt/\sqrt{2\pi} e^{-t^2/2}$, $H(x) := \int_x^\infty Dt$ and $\kappa := m\sqrt{p/(1-p)}$ were used.

At the transition the volume $\Omega$ shrinks to zero and the typical overlap $q$ between two different solutions $y$ approaches one. Keeping only the most divergent terms of (12) in this limit we find the following parametric representation of the critical line $\alpha_c(r^2)$ (see SM):

$$r^2 = \frac{1-p}{p} \frac{\kappa^2}{1-\alpha_c I(\kappa)}, \quad \alpha_c H(\kappa) = 1,$$  \hspace{1cm} (13)

where $I(\kappa) := \int_\kappa^\infty Dt(t-\kappa)^2$. This is the same result as found in [10] exploiting the properties of the Lyapunov function. The expression for the entropy (12) is rather similar to the one for the average entropy in the storage problem of a perceptron as obtained by Gardner [21]. In particular, for $r^2 = 0$ we find from (13) $\kappa = 0$ and therefore $\alpha_c = 2$, the classical result for the storage capacity of the perceptron.

**Conclusion.** We have shown that the phase transition in a high-dimensional version of MacArthur’s resource-competition model discovered recently by Tikhonov and Monasson is related to the existence of non-negative solutions of large random systems of linear equations. The starting point of our analysis is the observation that the “shielded” phase in which the species collectively regulate the resource demand to make all resources equally available is also characterized by the maximally possible number of surviving species set by the competitive exclusion principle. In contrast, in the “vulnerable” phase in which the species are susceptible to disturbances from the environment the number of surviving species remains below this margin. Since concentrations cannot be negative the difference between the two phases is related to the existence of non-negative solutions for species abundances realizing appropriate resource availabilities. The transition depends on the ratio between the number of variables and the number of equations, the density of non-zero entries in the coefficient matrix and the variance of the inhomogeneity vector. The existence of non-negative solutions to underdetermined linear equations is an active field of research in its own. While prevalent techniques require sparseness of the solutions [22,23] here we make—in the limit where the number of unknowns and the number of equations tend to infinity—also predictions for dense solutions.

Using Farkas’ Lemma the question on the existence of non-negative solutions to linear systems can be mapped onto a dual problem involving a set of linear inequalities. Using methods from the statistical mechanics of disordered systems we have analytically analyzed the typical properties of this dual problem in the thermodynamic limit. The result is in perfect agreement with numerical simulations, reproduces the transition line found by Tikhonov and Monasson, and points out an interesting connection with the storage problem of the single-layer perceptron. This link may indicate a way to further improvements in the quantitative characterization of large random ecosystems.

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