Collective Phase in Resource Competition in a Highly Diverse Ecosystem

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Organisms shape their own environment, which in turn affects their survival. This feedback becomes especially important for communities containing a large number of species; however, few existing approaches allow studying this regime, except in simulations. Here, we use methods of statistical physics to analytically solve a classic ecological model of resource competition introduced by MacArthur in 1969. We show that the nonintuitive phenomenology of highly diverse ecosystems includes a phase where the environment constructed by the community becomes fully decoupled from the outside world.

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Understanding the diversity of life-forms on our planet is an age-old question. Recent technological advances have uncovered that most habitats harbor hundreds of coexisting "species" (most of which are microbial [1–3]), and the problem of understanding such communities is currently at the forefront of the medical and environmental sciences [4–6]. One of the key obstacles arises from the fact that ecological and evolutionary time scales are generally not separable, giving rise to a coupled "ecoevolutionary dynamics" [7–9]. The fitness of an organism depends on its environment, but this environment is not fixed: it includes all other organisms in the community, is shaped by their activity, and changes on an ecological time scale. How to understand this feedback has long been recognized as an important question of community ecology [10].

A convenient example of such ecological feedback appears in models of resource competition [11]. The survival of an organism is determined by the availability of resources in its immediate environment. In quantitative theories of evolution (population genetics), we typically think of this environment as being fixed externally, but in an ecological setting, an experimentalist can only set the conditions faced by the community as a whole, e.g., the overall influx of resources. The immediate environment of an individual is affected by the activity of all other organisms and is not under our direct control. For example, consider increasing the overall influx of maltose (a sugar) to a multispecies bacterial culture. This could lead to an increase of maltose in the medium, opening the community to invasion by a species that grows well on this sugar. Alternatively, this could enable existing maltose-consuming species to expand in population, driving maltose availability back to the same level—or perhaps even depleting it further. The relation between the resources supplied to the community and the immediate environment seen by individual organisms is nontrivial. Our control extends on the former, but organism survival and, therefore, community structure are determined by the latter.

The mechanisms by which organisms shape their environment (niche construction theory [12]) have been the subject of much research, both at equilibrium (e.g., resource competition models [11]) and out of equilibrium (e.g., in the study of ecological successions [13]). Perhaps the most progress was achieved regarding the problem of resource competition in a well-mixed community at equilibrium, introduced 50 years ago by MacArthur [14]. However, the geometric approach developed by Tilman in his classic work [15] allowed him to analyze only the cases with $N = 1$ and $N = 2$ resources. It is not clear to what extent the intuition derived from low-dimensional models applies to the high-dimensional case. Recently, a simulation-based study of a modestly larger number of resources ($N = 10$) exhibited a surprising effect whereby a community interacting with another community would exhibit an effective "cohesion" even in the absence of any cooperative interactions between its members, purely as a consequence of environmental feedback [16]. The number of metabolites at play in a complex microbial community in nature is even larger, of the order $N \simeq 100$ [17,18]. It is an intriguing possibility that the phenomenology of high-diversity communities could contain qualitatively novel, nonintuitive regimes. However, few existing approaches allow studying niche construction or ecoevolutionary dynamics for a large number of interacting species, except in simulations.

The booming field of microbiome research is in dire need of a theoretical framework capable of describing complex communities, and there is a growing awareness that such a framework could emerge from the statistical physics of disordered systems [19–21]. In this Letter, we show that MacArthur's classic model of resource competition can be solved analytically in the limit of large N. We observe a phase transition between two qualitatively distinct regimes. In one regime, changes of external conditions propagate to the immediate environment experienced by organisms, as expected. However, in the other regime, the immediate environment of individuals becomes a collective property of the community, unaffected by the outside world. This regime, which is specific to high diversity, documents the emergence of a collective behavior as a consequence of large dimensionality.

In defining our model, we follow Ref. [16] but allow for more generality. Consider a multispecies community in a well-mixed habitat where a single limiting element $\mathcal{X}$ exists in N forms ("resources" $i \in \{1...N\}$). For example, this could be carbon-limited growth of bacteria in a medium supplied with N sugars. Let n_μ denote the population size of a species $\mu \in \{1, ..., \mathcal{S}\}$. Briefly, the availability h_i of each resource i in the immediate environment of individuals will determine the dynamics of n_μ. The changes in species abundance will translate into changes in the total demand for resources, denoted T_i. This total demand, in turn, will determine the resource availability h_i. This feedback loop is the focus of our analysis.

A species is characterized by its requirement χ_μ for the limiting element $\mathcal{X}$, and the "metabolic strategy" $\{\sigma_{\mu i}\}$ it employs to try to meet this requirement. We think of $\sigma_{\mu i}$ as the investment of species μ into harvesting resource i (e.g., the expression level of the corresponding metabolic pathway). Specifically, for a given resource availability $\{h_i\}$, the population growth rate of species μ is determined by the *resource surplus* Δ_μ experienced by its individuals:

$$\frac{dn_\mu}{dt} \propto n_\mu \Delta_\mu, \quad \text{with} \quad \Delta_\mu = \sum_i \sigma_{\mu i} h_i - \chi_\mu. \tag{1}$$

The first term is the total harvest of $\mathcal{X}$ from all sources, and the second is the requirement an individual must meet to survive. The proportionality coefficient is not important since we will only be concerned with the equilibrium state where $(dn_\mu/dt) = 0$.

Species abundances n_μ determine the total resource demand $T_i \equiv \sum_\mu n_\mu \sigma_{\mu i}$. This demand shapes the resource availability h_i. In the simplest model [16], organisms could be sharing a fixed total influx of resource R_i: $h_i(T_i) = R_i/T_i$. In his original formulation, MacArthur considered a more complex scenario of dynamical resources with renewal rate r_i and maximal availability K_i; this would correspond to setting $h_i(T_i) = K_i(1 - T_i/r_i)$; see Eq. (3) in Ref. [14]. In the interest of generality, here we will say only that the availability of resource i is a decreasing function of this total demand, $h_i = H_i(T_i)$, and allow the functions H_i to remain arbitrary, and possibly different for each resource.

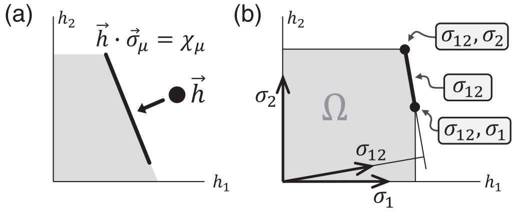

FIG. 1. The geometry of resource competition at $N = 2$. (a) If resource availability $\vec{h}$ lies above the line $\vec{h} \cdot \vec{\sigma}_\mu = \chi_\mu$, the species μ will multiply, depleting resources (see the arrow). (b) Competition between $\mathcal{S} = 3$ species; metabolic strategies are indicated by arrows (two specialists and one mixed strategy). The equilibrium $\vec{h}$ is always located at the boundary (highlighted) of the unsustainable region Ω; one or two species may coexist.

This model admits a convenient geometric formulation, where we can think of the metabolic strategies $\{\sigma_{\mu i}\}$ as $\mathcal{S}$ vectors in the N-dimensional space of resource availability. Each hyperplane $\vec{h} \cdot \vec{\sigma}_\mu = \chi_\mu$ separates this space into two regions [Fig. 1(a)]. Above this hyperplane, a positive resource surplus allows species μ to multiply. Below this hyperplane (the shaded region), resources are insufficient to support species μ. The intersection of such regions over all competing strategies $\{\vec{\sigma}_\mu, \chi_\mu\}$ defines the "unsustainable region" Ω:

$$\Omega = \bigcap_{\mu=1}^{\mathcal{S}} \{\vec{h} | \vec{h} \cdot \vec{\sigma}_\mu < \chi_\mu\}. \tag{2}$$

If resource availability $\vec{h}$ is inside Ω, no species can harvest enough resources to sustain its population. Outside Ω, at least one species can increase its abundance. Therefore, the equilibrium state can only be located at the boundary of Ω, which we denote $\partial\Omega$. The dynamics (1) possesses a Lyapunov function, which is convex and bounded from above, similar to the classic model of MacArthur—of which this is a generalization; see the Supplemental Material (SM) [22]. As a result, the equilibrium state always exists, is unique and stable, and can be found by solving a convex optimization problem over the region $\partial\Omega$. At this equilibrium, each species either is extinct and cannot invade ($n_\mu = 0$, $\Delta_\mu < 0$) or is present and its resource balance is met ($n_\mu > 0$, $\Delta_\mu = 0$).

Figure 1(b) shows an example at $N = 2$. Here, a community of two specialists, $\vec{\sigma}_1 = \{1,0\}$ and $\vec{\sigma}_2 = \{0,1\}$, both with cost χ_0, is exposed to a mixed strategy $\vec{\sigma}_{12} = \{x, 1 - x\}$, with a cost slightly below χ_0. The species $\vec{\sigma}_{12}$ will be able to invade and, depending on resource supply, may coexist with one of the specialists (but not both). The equilibrium will harbor one or two species, corresponding to the equilibrium $\vec{h}$ being located either at an edge or at a vertex of $\partial\Omega$.

The resource depletion rules H_i describe the external conditions: how much of each resource is supplied to the community as a whole. In contrast, $\vec{h}$ describes the availability of resources in the immediate environment of individuals, which ultimately dictates which species survive. Any set of competing strategies $\{\vec{\sigma}_\mu, \chi_\mu\}$ defines a unique community equilibrium and thus implements a mapping from external conditions into the actual environment $\vec{h}$. Our aim is to characterize the properties of this mapping.

The geometric intuition described above was first developed by Tilman [15], who exhaustively analyzed the cases $N = 1$ and $N = 2$. In higher dimensions, however, the enumeration of coexistence regimes for a given set of strategies, as in Fig. 1(b), quickly becomes a combinatorially difficult problem. In this Letter, we therefore adopt the statistical physics approach and characterize the expected properties of a *typical* community where the competing strategies are drawn out of some ensemble.

Specifically, for each species μ, we first pick its strategy as a random binary vector where each component $\sigma_{\mu i}$ is 1 with probability p, and 0 otherwise. The parameter p allows us to specify the location of a typical competitor on the specialist-generalist axis. We then draw a random cost $\chi_\mu = (\sum_i \sigma_{\mu i}) + \epsilon x_\mu$, where ϵ is a parameter (the cost scatter, assumed small), and x_μ is a Gaussian random variable of zero mean and unit variance. We set the total number of species to $\mathcal{S} \equiv \alpha N$.

The key simplification that makes the problem tractable analytically is the independence of $\vec{\sigma}_\mu$ and x_μ: the strategy and its cost are effectively uncorrelated. This assumption is strong, but far from unreasonable. First, it remains a good approximation even if a more complex cost model is considered (see Sec. 6 and Fig. S3 of the SM [22]), similar to the random energy model being a good approximation for low-lying states in other contexts, e.g., for the integer partitioning problem [23,24]. Second, the species competing for the same resources in real communities differ in evolutionary history, lifestyle, and physiology. Modeling the cumulative effect of these differences as a random contribution to the species' likelihood to succeed is arguably a better null model than claiming that the single factor we explicitly consider (the species' metabolic preference) plays the dominant role in determining its intrinsic performance.

Note that setting $h_i = 1$ satisfies the resource balance of all species within a quantity of order ϵ, so this cost model ensures that neither specialists nor generalists have an obvious advantage [16]. To characterize the fluctuations of resource availability $1 - h_i$, we introduce

$$m = \sum_i (1 - h_i), \qquad q = \sum_i (1 - h_i)^2. \tag{3}$$

The resource surplus of a typical species is given by

$$\langle \Delta_\mu \rangle = \left\langle \sum_i h_i \sigma_{\mu i} - \left(\sum_i \sigma_{\mu i} + \epsilon x_\mu \right) \right\rangle = -pm \tag{4}$$

(the angular brackets denote the mean over μ). Negative for most species, Δ_μ should hit zero for the lucky outliers who survive. We find that the spread of resource surplus values is given by $\psi \equiv \sqrt{p(1-p)q + \epsilon^2}$ (see the SM [22]). Intuitively, this is because species differ in cost (variance ϵ^2), and their strategy [$\{\sigma_{\mu i}\}$ with variance $p(1-p)$] picks out resources with different availability (with total squared deviation q). For this reason, rather than using q and m directly, for our order parameters, we choose ψ and the ratio $\lambda \equiv (pm/\psi)$.

Each particular set of competitors constitutes "frozen disorder," and the properties of a typical community can be computed using methods of statistical physics of disordered systems [25], as detailed in the SM [22]. For simplicity, all of the results will be quoted for the simplest supply model $H_i(T_i) = (R_i/T_i)$, where each resource is characterized by a single parameter: its total supply R_i (see the SM [22] for the general case). Our calculation yields explicit equations for the order parameters ψ and λ at equilibrium, in the thermodynamic limit $N, \mathcal{S} \to \infty$ at an α held constant:

$$\frac{1 - \alpha I(\lambda)}{1 - \alpha E(\lambda)} = 1 + (1 - p)\frac{\lambda}{\psi}$$
$$\psi^2[1 - \alpha I(\lambda)] = \epsilon^2 + p(1 - p)\overline{\delta R^2}[1 - \alpha E(\lambda)]^2. \tag{5}$$

Here, $\overline{\delta R^2}$ is the variance of resource supply R_i, and $I(\lambda) \equiv \int_\lambda^\infty (y - \lambda)^2 e^{-(y^2/2)} (dy/\sqrt{2\pi})$ and $E(\lambda) \equiv \int_\lambda^\infty e^{-(y^2/2)} \times (dy/\sqrt{2\pi})$ are auxiliary functions that can be expressed in terms of the error function erf.

The role of ϵ in our model is to measure how strongly a species' fate is influenced by intrinsic, rather than interaction-dependent (ecological) factors [16]. To study the equations above, consider first the limit $\epsilon \to 0$, where the scatter of intrinsic organism costs is negligible. In this limit, the parameter space separates into two phases [Fig. 2(a)]. One of these corresponds to the solution $\psi = 1 - \alpha E(\lambda) = 0$ and will be called the S phase; the other has $\psi \neq 0$ and will be called the V phase. The critical line [the dotted line in Fig. 2(a)] is described by

$$\overline{\delta R^2}_{\mathrm{crit}} = \frac{1 - p}{p} \frac{\lambda^2}{1 - \alpha_{\mathrm{crit}} I(\lambda)}, \qquad \text{where } \lambda = E^{-1}(1/\alpha_{\mathrm{crit}}).$$

For $\overline{\delta R^2} = 0$, the transition occurs at $\alpha_{\mathrm{crit}} = 2$, consistent with the perceptron phase transition [25,26].

To understand the physical meaning of these phases, consider first a community consisting of N perfect specialists with costs $\chi_\mu \equiv 1$. This community constitutes an example of the S phase, where the immediate environment of individuals is fully "shielded" from external conditions: faced with an uneven resource supply, species' abundance will adjust to drive resource availability to $h_i = 1$ for all i's, restoring symmetry. In general, a restricted set of species (small α) or a strongly heterogeneous resource supply (large $\overline{\delta R^2}$) will prevent the community from exactly matching demand to the uneven supply, and the externally imposed asymmetry between resources will propagate into the organisms' actual environment $\vec{h}$ (the V phase, "vulnerable" to external perturbations). However, as the community is exposed to new species [α is increased above the critical value; see the arrow in Fig. 2(a)], the community transitions into the shielded phase where the environment $\vec{h}$

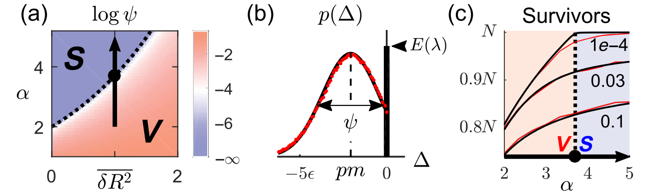

FIG. 2. (a) The phase transition at $\epsilon \to 0$. In the S phase, above a critical α (the dotted line), the fluctuations of resource availability vanish, shown here on log scale to highlight the transition. (b) The distribution of resource surplus at equilibrium. Black, the theoretical prediction; red, simulation data accumulated over 500 realizations at $N = 50$, shown for extinct species only (see the SM [22] for details). (c) The number of surviving species at equilibrium as a function of α at $\overline{\delta R^2} = 1$ [cf. the arrow in (a)] for three values of ϵ. Theoretical prediction (black); mean over 500 simulations at $N = 50$ (red); the standard error of the mean is too small to be visible. The deviation at $\epsilon = 10^{-4}$ is an effect of a small N. The dotted line is at critical α; shading labels the two phases.

is fully symmetric ($m = q = 0$) and is insensitive to external conditions.

To confirm this interpretation, consider the number of coexisting species at equilibrium. As we have seen, geometrically, this number is the codimension (N minus the dimension) of the region of $\partial\Omega$ where the equilibrium is located. Remarkably, this elusive quantity can also be computed analytically. Specifically, one can compute the distribution of the resource surplus Δ of all αN species at equilibrium [Fig. 2(b); see the SM [22]]:

$$p(\Delta) = \frac{1}{\sqrt{2\pi\psi^2}} e^{-[(\Delta+\lambda\psi)^2/2\psi^2]}\theta(-\Delta) + E(\lambda)\delta(\Delta). \tag{6}$$

Here, θ is the Heaviside function constraining Δ to be negative. The δ-shaped peak at $\Delta = 0$ represents the fraction of species whose resource demand is met. The number of survivors is therefore $\alpha N E(\lambda)$, in excellent agreement with simulations [Fig. 2(c)]. The S phase where $\alpha E(\lambda) = 1$ therefore harbors a complete set of exactly N species. If the perturbation of external conditions is small, no species will go extinct. Since the vectors h_i and χ_μ (μ running over N surviving species) are related by a full-rank matrix $\sigma_{\mu i}$, the resource availability at the new equilibrium will remain exactly the same, confirming our interpretation of this shielded phase.

For a nonzero ϵ, the strict phase transition is replaced by a crossover [Fig. 3(a)]. At large ϵ, community structure is no longer shaped by interactions between community members; instead, it becomes dominated by species who outperform others in all circumstances, and the environmental feedback studied here becomes irrelevant [16]. For small ϵ's, however, the distinct features of the shielded and vulnerable phases remain clearly recognizable: the fluctuations of resource availability are, respectively, of order ϵ or much larger than ϵ [Fig. 3(b)].

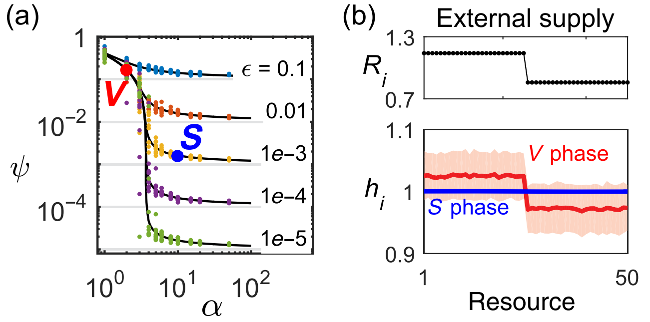

FIG. 3. (a) At finite ϵ, the phase transition is replaced by a crossover. Theoretical curves are overlaid with simulation data points for a range of α (ten instances each). At large α, we observe $\psi \to \epsilon$, confirming that the fluctuations of h_i become negligible. (b) The qualitative distinction between phases persists at finite ϵ. Here, simulation results are shown for $\epsilon = 10^{-3}$. (Upper panel) A community faces a bimodal supply of $N = 50$ resources. (Lower panel) The equilibrium availability of resources h_i (mean ± standard deviation over 500 instances) for two values of α corresponding to different phases [highlighted in (a)]. In the shielded S phase, the asymmetry of the external supply does not affect the resource availability h_i.

This result has intriguing implications. Consider a community facing the strongly uneven resource supply shown in Fig. 3(b) (top panel). Define a species' individual performance as its growth rate when placed in this environment, with no other organisms present. One might expect this performance metric to be predictive of species' survival in a community setting: surely, increasing the supply of maltose to a community should favor organisms that grow well on maltose. In the more intuitive V phase, this expectation is indeed correct. However, in the S phase, the internal environment becomes a collective property governed by the statistical properties of the species' pool, rather than by the external conditions [Fig. 3(b), bottom panel]. As a result, the performance measured in external conditions becomes irrelevant: it no longer predicts whether a species will survive (see Fig. S4 of the Supplemental Material [22]).

In ecological terms, the model considered here was purely competitive: increasing the abundance of any species reduces the growth rates of everyone else; i.e., there are no "cooperative interactions." Nevertheless, we have shown that, at high dimension, the parameter space of this classic resource competition model contains a strongly collective regime. These conclusions were drawn in the context of a particular, highly simplified model. Specifically, our analysis ignored spatial structure, assumed deterministic dynamics, and focused on equilibrium states only. The nonstationary nature of real communities is famously one of the key factors promoting and maintaining ecological diversity, and it is missed by an equilibrium model [27]. Stochasticity and spatial structure are also tremendously important in most contexts, especially if evolutionary aspects are taken into consideration [28]. Nevertheless, the goal of this Letter was to explore specifically the feedback of organisms onto their environment and identify the implications of large dimensionality. For this purpose, the simplified model adopted here provides a convenient starting point, and highlights the promise of applying statistical physics to gain analytical insight into the nonintuitive phenomenology of large-dimensional metabolic networks [29] and highly diverse ecosystems. The mean-field nature of our model allows us to hope that the techniques of out-of-equilibrium statistical physics of disordered systems could also provide some insight into its dynamical behavior.

In other fields of theoretical biology, e.g., neuroscience and learning theory, statistical physics has already uncovered a wealth of phenomena that could never be understood from sketches of "which neuron activates which neuron." In ecology, we can expect its impact to be equally dramatic, yet this direction remains underexplored; see, however, recent works [19–21]. An important novelty of our approach was to focus on function, rather than composition. Currently, the terms "large-N ecology" evoke primarily the investigation of mechanisms of coexistence, starting from the classic work of May [30]. By contrast, our main goal here was to characterize a *functional* consequence of ecological dynamics, namely, the environment that a community shapes for itself.

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