Beyond May: Complexity-stability relationships in disordered dynamical systems

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Robert May famously used random matrix theory to predict that large, complex systems cannot admit stable fixed points. However, this general conclusion is not supported by empirical observation: from cells to biomes, biological systems are large, complex—and, by and large, stable. In this paper, we revisit May's argument in the light of recent developments in both ecology and random matrix theory. Using a non-linear generalization of the Lotka-Volterra model, we show that there are in fact two kinds of complexity-stability relationships in disordered dynamical systems: if self-interactions grow faster with density than cross-interactions, complexity is destabilizing; but if cross-interactions grow faster than self-interactions, complexity is stabilizing. Our result shows that May's principle that "complexity begets instability" is not a general property of complex systems; instead, it is a property of a subclass of weakly cross-regulated disordered systems.

Introduction.—Few mathematical arguments have influenced biological thinking like May's prediction that large, complex ecosystems cannot be stable [1]. It is, on the face of it, a perplexing conclusion. On the one hand, May's mathematical argument is simple and seemingly model-free, suggesting universal applicability, also beyond biology [2, 3]. On the other hand, it is clear that at least some large, complex systems are stable—else which regularities would biology be studying in the first place? In fact, empirical observation suggests the opposite relationship between complexity and stability: species-rich, strongly-coupled communities such as rainforests tend to be stable over time, while sparser ones, for instance arctic communities, often exhibit large fluctuations, extinctions, and invasions [4–6]. The tension between May's theoretical argument and observation is at the center of the longstanding "diversity-stability debate" in ecology [7, 8].

May's argument can be summarized as follows [1]. Consider a system with N populations x_i, characterized by an equilibrium point $\mathbf{x}^*$. Near that equilibrium $\mathbf{x} = \mathbf{x}^* + \delta\mathbf{x}$, the dynamics of the system is described by linear equations $d(\delta\mathbf{x})/dt = A(\delta\mathbf{x})$, and the stability of these equations requires that all eigenvalues of A have negative real part. But if A can be represented as $A = B - I$, where B consists of random, independent interactions (with zero mean and variance σ^2), and $-I$ corresponds to stabilizing self-interactions on some natural timescale, then the circular law of random matrix theory implies that all eigenvalues of A will have negative real part only if $\sigma^2 N < 1$. This places a sharp constraint on both diversity N and interaction strength σ, often referred to as "complexity begets instability". (This argument generalizes to $\langle B_{ij} \rangle \neq 0$, incomplete connectivity,

or correlated interactions [9].)

Many authors have sought to ease the tension between May's prediction and empirical observation by invoking effects not captured by dynamical systems with random coefficients [7, 10–14]. In this letter, we use recent results in the physics of disordered systems [15, 16] to show that May's argument itself is incomplete: in random dynamical systems, stability does not necessarily decrease with dimensionality and interaction strength—the opposite behavior is also possible, without the need for special or additional structure. For an in-depth discussion of the ecological implications of our result, see [17].

Model.—Consider the dynamical system in N variables

$$\dot{x}_i = f(x_i) - \sum_j A_{ij} g(x_i) h(x_j) \,. \tag{1}$$

Here $f(x_i)$ represents the self-dynamics of a population i (growth and self-regulation), while $g(x_i)$ and $h(x_j)$ capture the cross-interaction of i with other populations. That interaction is weighted by a coefficient A_{ij}, such that $A_{ij} > 0$ (resp. $A_{ji} < 0$) implies a negative (resp. positive) effect of j on the growth of i. Non-zero diagonal elements A_{ii} accounts for additional self-interactions with the same functional form as cross-interactions. We refer to f as the "production function" and g as the "response function".

This general setting has been used to study universality in network dynamics [18] and to construct minimal models of complex dynamics [19], with applications ranging from biological [20, 21] to social [22–24] systems. The classic generalized Lotka-Volterra (GLV) competition model studied recently by Bunin and collaborators [25, 26] corresponds to f, g, h all linear.

However, it is natural both physically and biologically to consider more general functions, including power laws $f(x) \sim x^\alpha$, $g(x) \sim x^\beta$, $h(x) \sim x^\gamma$. From a physical perspective, we can imagine populations x_i forming three-dimensional clusters whose growth is limited to their two-dimensional surface, leading to a production function $f(x) \sim x^{2/3}$. Biologically, the growth of organisms (populations of cells) has long been known to scale like $f(x) \sim x^k$ with $k \simeq 3/4$ [27], which can be understood in terms of hydrodynamic constraints on vascular and pulmonary networks. For reasons that are not currently understood, a similar pattern of growth appears to recur at the level of ecological communities [17, 28]. In a different direction, it has been recently suggested that predator-prey interactions can be modelled with a square root law, i.e. $g(x) \sim h(x) \sim x^{1/2}$ [29, 30].

Homogeneous interactions.—Under what condition does (1) admit a (linearly) stable equilibrium? We begin with the simple case where all self-interactions have the same strength $A_{ii} = \mu_s$, and similarly for cross-interactions $A_{ij} = \mu$ ($i \neq j$). Defining

$$\psi(x) \equiv (\mu_s - \mu) - \left(\frac{f'(x)}{f(x)} - \frac{g'(x)}{g(x)} \right) \frac{f(x)}{g(x)h'(x)}, \quad (2)$$

an elementary calculation shows that stability of the homogeneous equilibrium $x_i^* = x^*$ requires $\psi(x^*)g(x^*)h'(x^*) > 0$, or $\psi(x^*) > 0$ if we assume that g and h are positive, increasing functions. This stability condition involves the relative strength of diagonal and off-diagonal interactions ($\mu_s - \mu$), but also on the relative growth rate of the production and response functions near the equilibrium ($f'(x^*)/f(x^*) - g'(x^*)/g(x^*)$).

With power laws, the condition $\psi(x^*) > 0$ evaluates to

$$(\alpha - \beta)(N - 1) < \gamma(\mu_s/\mu - 1) - (\alpha - \beta)(\mu_s/\mu), \quad (3)$$

leading to three different regimes:

- If $\alpha = \beta$, stability requires $\mu_s > \mu$, i.e. self-interactions must be stronger than cross-interactions. This is the usual conclusion drawn from the Lotka-Volterra model.

- If $\alpha > \beta$, stability places an upper bound on N: the more complex the system, the less likely to be stable. We can call this "May" behavior.

- If $\alpha < \beta$, stability places an lower bound on N: the more complex the system, the more likely to be stable. This is "anti-May" behavior.

Random interactions: stability condition.—We now consider the case of random interactions. Specifically, we assume that interaction coefficients A_{ij} are drawn independently from a distribution with mean μ and standard deviation σ; We assume the diagonal elements A_{ii} have a mean value μ_s (possibly different from μ) but the same standard deviation σ.
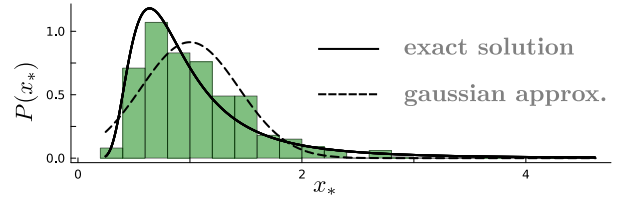

FIG. 1: The equilibrium distribution with power-law self- and cross-interactions is accurately reproduced by Eq. (12) and its Gaussian approximation. For simulations (in green) we used $\alpha = 1$, $\beta = 3/2$, $\gamma = 1$, $N = 50$, $\mu = \mu_s = 10^{-2}$, $\sigma = 5 \cdot 10^{-3}$.

We compute the Jacobian matrix at equilibrium

$$J_{ij}^* = -A_{ij}g(x_i^*)h'(x_j^*) \qquad \text{for } i \neq j \qquad (4)$$
$$J_{ii}^* = f'(x_i^*) - g'(x_i^*)f(x_i^*)/g(x_i^*) - A_{ii}g(x_i^*)h'(x_j^*) , \qquad (5)$$

where we used $\sum_j A_{ij}h(x_j^*) = f(x_i^*)/g(x_i^*)$. In order to investigate the spectral properties of J^*, we follow Stone [31] in using a recent generalization of the circular law in random matrix theory [15].

In Ref. [15], Ahmadian *et al.* consider matrices of the form $M + LSR$, where M, L and R are deterministic matrices, and S is a random matrix with i.i.d. coefficients, zero mean and variance σ^2. They show that eigenvalues of large matrices of this form are contained in the complex domain $\mathcal{D} = \{ \zeta \in \mathbb{C}, \text{Tr}[(\Psi(\zeta)\Psi(\zeta)^\dagger)^{-1}] \geq \sigma^{-2} \}$, where $\Psi(\zeta) = L^{-1}(M - \zeta I)R^{-1}$. If L, R and M are all diagonal $N \times N$ matrices, the equation of $\mathcal{D}$ simplifies to

$$\sum_{i=1}^N \left| \frac{M_{ii} - \zeta}{L_{ii}R_{ii}} \right|^{-2} \geq \sigma^{-2}. \qquad (6)$$

To use this result, we decompose the interaction matrix as $A = \mu\mathbf{1} + (\mu_s - \mu)I + S$, with $\mathbf{1}$ the matrix with all entries equal to 1 and S a random matrix as defined above. Up to the rank-one perturbation $\mu\mathbf{1}$ which does not affect stability properties [31], we can write the Jacobian (4) as $J = M + LSR$ with diagonal matrices

$$M_i = -g(x_i^*)h'(x_i^*)\psi(x_i^*), \quad L = g(x_i^*), \quad R = h'(x_i^*), \qquad (7)$$

where $\psi(x)$ is the function defined in (2). Stability of the equilibrium requires that $\mathcal{D}$ be entirely contained in the left half-plane (all eigenvalues have negative real part). For this to hold, it is no longer sufficient that $\psi(x_i^*) > 0$ for each i: we must also have that $0 \notin \mathcal{D}$, hence from (6):

$$\sum_{i=1}^N \left(\frac{\sigma}{\psi(x_i^*)} \right)^2 < 1. \qquad (8)$$

In the GLV model, $\psi(x) = \mu_s - \mu$ (independently of x) and we recover the classical condition $\sigma\sqrt{N} < (\mu_s - \mu)$
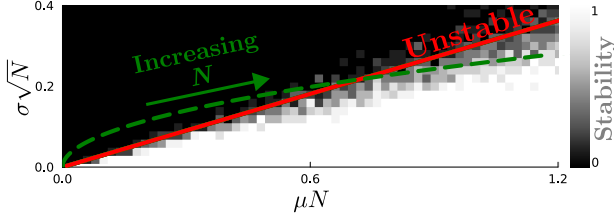
FIG. 2: For a system in the "anti-May" phase, an increase in N, corresponding to moving along $\sqrt{N}$ in the $(\sigma\sqrt{N}, \mu N)$ plane (green dashed line), will be stabilizing rather than destabilizing. Here we show results from the numerical resolution of the dynamical system (1). Stability is defined as full stable coexistence. The red line is computed obtained using DMFT and the generalized stability condition $N\langle(\sigma/\psi)^2\rangle < 1$. Parameters values are $\alpha = 1$, $\beta = 3/2$, $\gamma = 1$, $N = 50$ and 10 replicates for the simulations. The green line was plotted for $\mu = 0.1$ and $\sigma = 0.75$.

[32]. In general, however, the dependence on equilibrium values x_i^* (which in turn depend on N) does not cancel out, and one must gain information about the distribution of equilibrium values $P(x_i^*)$ to assess the stability condition (8).

Random interactions: equilibrium distribution.— Henceforth we assume $f(x_i) = x_i^\alpha$, $g(x_i) = x_i^\beta$, $h(x_i) = x_i^\gamma$. (Any coefficients can be reabsorbed in the statistics of A and by a rescaling of time.) Following e.g. Ref. [16], we can derive from the evolution equation (1) a dynamical mean field theory (DMFT) which describes the ensemble of $N \gg 1$ variables by means of a single, self-consistent representative stochastic trajectory

$$\dot{x} = x^\alpha - A_s x^{\beta+\gamma} - x^\beta\left(\mu N\langle x^\gamma\rangle + \sigma\sqrt{N}\eta\right), \quad (9)$$

where A_s is a random variable with the statistics of A_{ii} and η is a Gaussian noise with zero mean and correlation $\langle x^\gamma(t)x^\gamma(s)\rangle$. At equilibrium, we can write

$$x_*^{\alpha-\beta} - A_s x_*^\gamma = \left(\mu N\langle x_*^\gamma\rangle + \sigma\sqrt{N\langle x_*^{2\gamma}\rangle}\xi\right), \quad (10)$$

where ξ is now a standard normal random variable. The equation above can be solved for x_* for specific values of $(\alpha - \beta)/\gamma$, or if $A_s = 0$. (In the following we show that neglecting A_s even when it is not zero does not affect noticeably the quality of the approximation.) In this case the stationary solution is given by

$$x_* = \left(\mu N\langle x_*^\gamma\rangle + \sigma\sqrt{N\langle x_*^{2\gamma}\rangle}\xi\right)^{1/(\alpha-\beta)}. \quad (11)$$

The equilibrium distribution $P(x_*)$ can then be obtained as the pushforward of the distribution of ξ:

$$P(x_*) = \frac{|\alpha - \beta|x_*^{\alpha-\beta-1}}{\sqrt{2\pi\sigma^2 N\langle x_*^{2\gamma}\rangle}}\exp\left\{-\frac{(x_*^{\alpha-\beta} - \mu N\langle x_*^\gamma\rangle)^2}{2\sigma^2 N\langle x_*^{2\gamma}\rangle}\right\}, \quad (12)$$
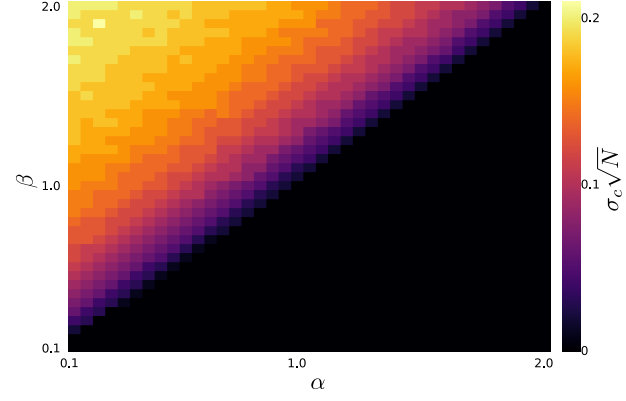

FIG. 3: The "May" and "anti-May" phases derived in the case of uniform interactions ($\sigma = 0$) are robust with respect to random interactions ($\sigma > 0$). Here we simulated system (1) in the power law case for a fixed value of $\mu = \mu_s = 10^{-2}$, $\gamma = 1$, $N = 100$ and 100 replicates, and we evaluated σ_c, defined here as the value above which full stable coexistence is less probable than 50%, at varying α and β. No amount of heterogeneity is allowed in the bottom right triangle because we have $\mu = \mu_s$, while an increasing value of σ_c is found as β becomes larger than α. We stress that the existence of a finite $\sigma_c\sqrt{N}$ above which instability is triggered also in the upper triangle, does not imply that increasing N will destabilize the system, because μN would also change.

where the expectation values must be computed self-consistently.

Equipped with the equilibrium distribution $P(x^*)$, we can compute, for given N and μ, the maximal heterogeneity σ_c compatible with the linear stability condition $N\langle(\sigma/\psi(x^*))^2\rangle < 1$.

Let us focus on the choice $\alpha = 1$, $\beta = 3/2$ and $\gamma = 1$, with $A_s = 0$. In this case the first and second moments formally diverge. This is not truly problematic because we are dealing with large, but *finite* populations. Following [17, 33] and assuming $\sigma\sqrt{N\langle x_*^2\rangle} \ll \mu N\langle x_*\rangle$, we can expand the solution (11) to first order in $\sigma\sqrt{N\langle x_*^2\rangle}$, and approximate (12) with a Gaussian distribution with moments $\langle x_*\rangle = (\mu N)^{-2/3}$ and $\langle x_*^2\rangle = (\mu N)^{-4/3}/(1 - 4(\mu N)^{-2}\sigma^2 N)$.

The result is plotted against simulations in Fig. 1. We show both the exact solution (12) (where integration for the moments has been performed up to a maximum value above which no equilibrium value should be found) and the Gaussian approximation. Simulations correspond to $A_s = \mu$, showing that neglecting the A_s term in analytical expressions does not introduce a significant error.

The properties of large random dynamical systems is often portrayed in the $(\sigma\sqrt{N}, \mu N)$ plane [25]. Everything else being fixed, an increase of the number of degrees of freedom N moves the system along a square-root trajec-

tory in that plane. In the GLV model, the boundary between the stable and unstable parameter regions is the horizontal line $\sigma_c \sqrt{N} = \mu_s$ [25], hence stability is never possible at large N.

In Fig. 2 we plot the stability condition $N \langle (\sigma/\psi(x^*))^2 \rangle < 1$ for $\alpha = 1$, $\beta = 3/2$ derived from (12) (solid line) together with results from simulations (shading). Here, because the boundary between the stable and unstable phases is a straight line with positive slope, increasing N will eventually bring the system in the stable region. This behavior corresponds to the "anti-May" phase defined previously.

Finally, Fig. 3 shows results of simulations for $\sigma_c \sqrt{N}$ in the (α, β) plane, at fixed μN and $\gamma = 1$. (Numerically, we define $\sigma_c \sqrt{N}$ as the value of σ above which full stable coexistence has a probability lower than 50%.) In these simulations we use $\mu_s = \mu$, which would never be stable in the GLV model. Fig. 3 illustrates the transition between a "May" phase for $\alpha \geq \beta$ and an "anti-May" phase for $\alpha < \beta$, showing that our analytical results are robust to heterogeneous interactions.

Discussion.—The relationship between complexity and stability in high-dimensional dynamical systems has been a longstanding puzzle, in ecology and in other fields. In this letter, we have showed that the condition $\sigma \sqrt{N} < \mu_s - \mu$ (popularized by May's slogan "complexity begets instability") does not provide a complete picture of the relationship between complexity and stability. In particular, we have seen that the generalized Lotka-Volterra model, often cited in support of May's general prediction, exemplifies a special cancellation in the more general stability condition $N \langle (\sigma/\psi)^2 \rangle < 1$. In models where self-interactions grow faster than cross-interactions, the opposite behavior is observed: stability becomes *more* likely with increasing diversity N.

Future work can look at the case where two-body interactions are not separable, or include higher order interaction to generalize the results in Ref. [34] based on the GLV model.

The Julia code used for simulations is available at `www.github.com/msmerlak/beyond-may`.

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