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Editors' Suggestion

Properties of Equilibria and Glassy Phases of the Random Lotka-Volterra Model with Demographic Noise

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We study a reference model in theoretical ecology, the disordered Lotka-Volterra model for ecological communities, in the presence of finite demographic noise. Our theoretical analysis, valid for symmetric interactions, shows that for sufficiently heterogeneous interactions and low demographic noise the system displays a multiple equilibria phase, which we fully characterize. In particular, we show that in this phase the number of locally stable equilibria is exponential in the number of species. Upon further decreasing the demographic noise, we unveil the presence of a second transition like the so-called "Gardner" transition to a marginally stable phase similar to that observed in the jamming of amorphous materials. We confirm and complement our analytical results by numerical simulations. Furthermore, we extend their relevance by showing that they hold for other interacting random dynamical systems such as the random replicant model. Finally, we discuss their extension to the case of asymmetric couplings.

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Lotka-Volterra equations describing the dynamics of interacting species are key to theoretical studies in ecology, genetics, evolution, and economy [1–6]. Cases in which the number of species is very large are becoming of general interest in disparate fields such as ecology and biology, e.g., for bacteria communities [7,8], and economics, where many agents trade and interact simultaneously in financial markets and in complex economic systems [9,10].

The theoretical framework used in the past for a small number of species is mainly based on the theory of dynamical systems [11–16]. When the number of ordinary differential equations associated with the Lotka-Volterra (LV) model becomes very large, i.e., for many species, methods based on statistical physics are ideally suited. Indeed, several authors have recently investigated different aspects of community ecology—such as properties of equilibria, endogeneous dynamical fluctuations, and biodiversity—using ideas and concepts rooted in statistical physics of disordered systems [5,17–27]. Similar investigations have been also performed for economic systems [28]. Dealing with a large number of interacting species can actually become a welcome new ingredient conceptually and methodologically. In fact, qualitatively new collective behaviors, classified into "phases," can emerge. Also, as it happens in physics, such phases are not tied to the specific model they come from; instead, they characterize whole classes of systems in a generic way, potentially including natural systems [29]. From this perspective, it is interesting to ask which kind of different collective behaviors arise for LV models in the limit of many interacting species and what are their main properties [19,20]. These questions, which have started to attract a lot of attention recently, tie in with the analysis of the properties of their equilibria [30–32].

Here, we focus on the disordered Lotka-Volterra model of many interacting species, which is a representative model of a well-mixed community ecology [33] that can be mapped or related to models used in evolutionary game theory and for economic systems [28,34–37]. We consider the case of symmetric interactions and small immigration that, allowing for an appropriate interplay with demographic noise, ensures that all species are present, and work out the phase diagram as a function of the degree of heterogeneity in the interactions and the strength of the demographic noise. Compared to previous works [5,19,20,38], adding demographic noise not only allows us to obtain a more general picture but also to fully characterize the phases and connect their properties to the ones of equilibria. In particular, we shall show that the number of locally stable equilibria in the LV model is exponential in the system size and their organization in configuration space follows general principles found for models of mean-field spin glasses. Our findings, although obtained for symmetric interactions, provide a useful starting point to analyze the nonsymmetric case, as we shall demonstrate by drawing general conclusions on properties of equilibria in the case of mild asymmetry.

The disordered Lotka-Volterra model for ecological communities [5,19] with random interactions α_{ij} between species is defined by this equation:

$$\frac{dN_i}{dt} = N_i\left[1 - N_i - \sum_{j,(j\neq i)} \alpha_{ij} N_j\right] + \eta_i(t). \tag{1}$$

The elements of the random matrix α_{ij} are independent and identically distributed variables such that, for $i < j$,

$$\text{mean}[\alpha_{ij}] = \mu/S \ \text{var}[\alpha_{ij}] = \sigma^2/S \tag{2}$$

with $\alpha_{ij} = \alpha_{ji}$, as we focus on the symmetric case (i runs from 1 to the total number of species S). $N_i(t)$ is the relative abundance of species i at time t, meaning that the population is normalized with respect to the total number of individuals N_{ind} that would be present in the absence of interactions; $\eta_i(t)$ is a Gaussian noise with zero mean and covariance $\langle \eta_i(t)\eta_j(t')\rangle = 2TN_i(t)\delta_{ij}\delta(t-t')$, where $T = (1/N_{\text{ind}})$. This multiplicative noise term, for which we follow Ito's convention, allows us to include the effect of the demographic noise in a continuous setting [39–41], which is the larger the global population, the smaller the strength T of the demographic noise.

Immigration from the mainland is modeled by a reflecting wall for the dynamics at a cutoff value for the species abundances $N_c = \lambda$; this is more practical for simulations than the usual way of adding a λ in the rhs of Eq. (1) (see the Supplemental Material [42], Sections VI and VII, for more details). As shown in [20], the stochastic process induced by Eq. (1) admits an equilibriumlike stationary Boltzmann distribution with associated temperature T:

$$P(\{N_i\}) = \exp\left(-\frac{H(\{N_i\})}{T}\right), \tag{3}$$

where in this specific case the Hamiltonian is

$$H = -\sum_i \left(N_i - \frac{N_i^2}{2}\right) + \sum_{i<j} \alpha_{ij} N_i N_j + \sum_i [T \ln N_i - \ln \theta(N_i - \lambda)]. \tag{4}$$

The before-last term is due to the demographic noise and the last one to the reflecting wall, which leads to a lower immigration cutoff at $N_i = \lambda$ [$\theta(x)$ is the Heaviside function]. By taking advantage of this mapping to an equilibrium statistical mechanics problem and by using theoretical methods developed for disordered systems, we obtain the properties of the stationary states and the equilibria of the LV model from the analysis of the equilibrium states and the local minima of the energy function H. Our theoretical framework is based on the replica method [43], which represents a well-established technique to obtain exact equations for the order parameters in disordered systems. The working strategy consists in computing the replicated free energy $f = -\lim_{S\to\infty}(T/S)\overline{\ln Z}$ by writing down the disordered average of the replicated partition function $\overline{Z^n}$. In this setting, one has to study n distinct copies of the original system (the replicas) and eventually take the analytical continuation $n \to 0$. The computation is described in full detail in the Supplemental Material (SM).

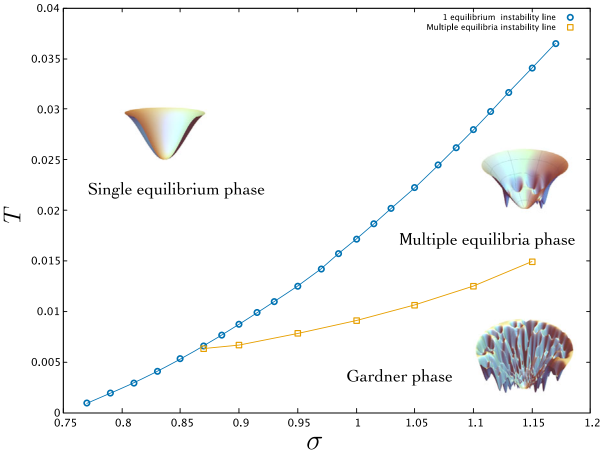

FIG. 1. Phase diagram showing the strength of the demographic noise T as a function of the degree of heterogeneity σ at fixed $\mu = 10$ and selected value of the cutoff $N_c = 10^{-2}$. Upon decreasing the noise, three different phases can be detected: (i) a single equilibrium phase, (ii) a multiple equilibria regime between the light blue and the orange lines, and (iii) a Gardner phase, which turns out to be characterized by a hierarchical organization of the equilibria in the free-energy landscape.

Among the most important results is the existence of three distinct phases for the LV model in presence of demographic noise and small but nonzero immigration, as shown in Fig. 1 (we focus on $\lambda = 10^{-2}$; similar results are obtained for smaller values of λ). We find no sensitive dependence on the average interaction parameter, so the phase diagram has been obtained at fixed value $\mu = 10$.

For large enough demographic noise (corresponding to high temperature), we find that there is a single equilibrium phase, i.e., the noise is so strong that the interactions within species do not play an important role and for any initial condition the system relaxes toward a unique stationary state with fluctuating equilibrium dynamics. When the strength of the demographic noise decreases, multiple states emerge. This outcome offers a useful picture in the study of microbial communities provided that sufficiently large species abundances are taken into account [62–64].

We can study this transition by analyzing the stability of the thermodynamic high-temperature phase. This is performed by analyzing its free-energy Hessian matrix $\mathcal{H}$. The point at which the lowest eigenvalue (the so-called "replicon" eigenvalue in the replica framework) of $\mathcal{H}$ reaches zero signals the limit of stability of the high-temperature phase through a continuous second-order phase transition and the emergence of multiple equilibria.

Within the replica method that we used here, the appearance of a zero replicon mode corresponds to the breaking of replica symmetry. This condition leads to an equation for the transition line that corresponds to the blue curve in Fig. 1:

$$\lambda_R = (\beta\sigma)^2[1 - (\beta\sigma)^2\overline{(\langle N_i^2\rangle - \langle N_i\rangle^2)^2}] = 0, \qquad (5)$$

where $\beta = 1/T$. The average $\langle\cdot\rangle$ is the thermodynamics average taken over the effective Hamiltonian [Eq. (4)], while $\bar{\cdot}$ denotes the average over the quenched disorder associated with the random interactions (i is a dummy index since statistically all species are equivalent after average over the interactions). Physically, the condition above can be shown to correspond to a diverging response function [19,20] and is a signature of the system being at the edge of stability, namely at a "critical point" in the parameter space [65].

Below the blue curve, there exist multiple states. Which one is reached dynamically depends on the initial condition. Such states correspond to dynamically fluctuating equilibria that are locally stable to perturbations and that have typically an overlap in configuration space given by $q_0 = (1/S)\sum_i \langle N_i\rangle_\alpha \langle N_i\rangle_\beta$, where α and β denote the average within two generic states α and β. One can similarly define the intrastate overlap $q_1 = (1/S)\sum_i \langle N_i\rangle_\alpha^2$. See Fig. 2 for a pictorial representation of these two quantities and the organization of equilibria in phase space. This is (in the replica jargon) the so-called one-step replica symmetry breaking phase (1RSB). In order to characterize the properties of this phase of the LV model, we have computed the number of states, and hence of equilibria, using methods developed for structural glasses [56]. More specifically, we have computed the complexity Σ (see Section IV of the SM for details), which is defined as the logarithm of the number of equilibria with a given free-energy density f normalized by the number of species S. This allows us to show that the number of equilibria below the blue line in Fig. 1 is *exponential* in S, i.e., there is a strictly positive complexity Σ. This outcome turns out to be particularly timely in light of ecological resilience and stability landscape concepts, notably in relation to recent findings on microbial communities [67–69].

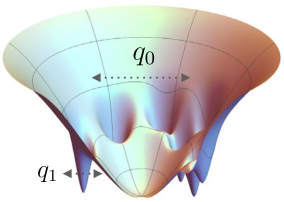

FIG. 2. Cartoon of the landscape in the 1RSB ansatz. The parameters q_0 and q_1, which can be exactly obtained by solving saddle-point equations, are respectively associated with the size of the largest basin and the innermost basin (large overlaps are associated with small basins).

When decreasing further the demographic noise, the heterogeneity in the interactions becomes even more important and a second phase transition takes place. In order to locate it, we repeat exactly the same procedure as for the single equilibrium phase but now within one of the typical states with a given free-energy f [70]. The computation is more involved: it corresponds to analyzing the stability of the 1RSB ansatz (all technical details of the calculation are reported in the SM).

The critical temperature that results from the equation above leads to the orange line in Fig. 1. Crossing this line results in a fragmentation of each state into a fractal structure of sub-basins [71] (see the landscape on the bottom in Fig. 1): each state becomes a metabasin that contains many equilibria, all of them marginally stable, i.e., poised at the edge of stability [20], and organized in configuration space in a hierarchical way, as in the case of mean-field spin glasses [43]. This phase, which is called "Gardner," plays an important role in the physics of jamming and amorphous materials [72,73]. Our results unveil its relevance in theoretical ecology by showing that it describes the organization of equilibria in the symmetric disordered LV model at low enough demographic noise and for highly heterogeneous couplings.

We now present numerical simulation results that confirm and complement our analytical study. Simulating LV dynamics in the presence of demographic noise is a challenging algorithmic task. In order to reach long times, we have used and generalized a sophisticated method introduced in the context of directed percolation [61] (see Section VII of the SM for details). The initial condition is set by drawing independently each species abundance in [0, 1].

There are three sources of randomness for a given sample: the interactions, the initial conditions, and the demographic noise. In the following, we obtain numerically the average correlation function defined by

$$\mathbb{E}[N(t)N(t')] = \frac{1}{SN_{\text{sample}}}\sum_{i=1}^{S}\sum_{r=1}^{N_{\text{sample}}} N_i^r(t)N_i^r(t'), \qquad (6)$$

where $\mathbb{E}[X]$ stands for the average over all those sources of randomness. If both the system size and the sampling set are sufficiently large ($S \gg 1$ and $N_{\text{sample}} \gg 1$), it can be shown that the stochastic process converges in law [57]. We show results for $S \sim 500$ and $N_{\text{sample}} \sim 50$. We have verified that these values are large enough to guarantee that there is no (S, N_{sample}) dependency for the correlation functions. We find that in the high-temperature phase a time translationally invariant state is reached after a finite timescale t_{wait}:

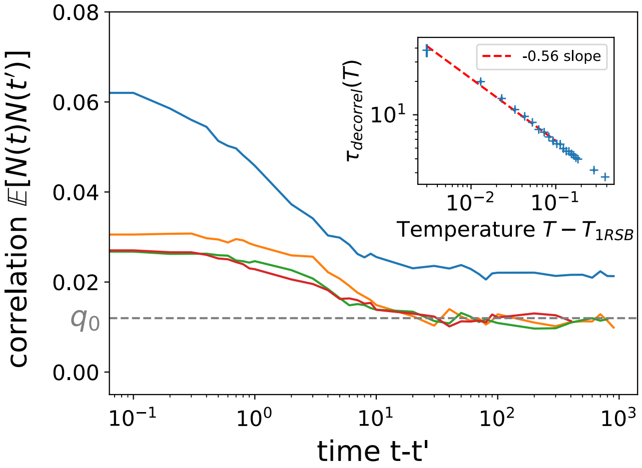

FIG. 3. Correlation $C(t, t')$ as a function of $t - t'$ in the one-equilibrium phase for different t': $t' = 1$ (blue), 10 (orange), 100 (green), 500 (red). The inset shows the decorrelation time versus $(T - T_{1\mathrm{RSB}})$ in log-log scale. The blue points correspond to numerical data, while the dashed red line is a fit.

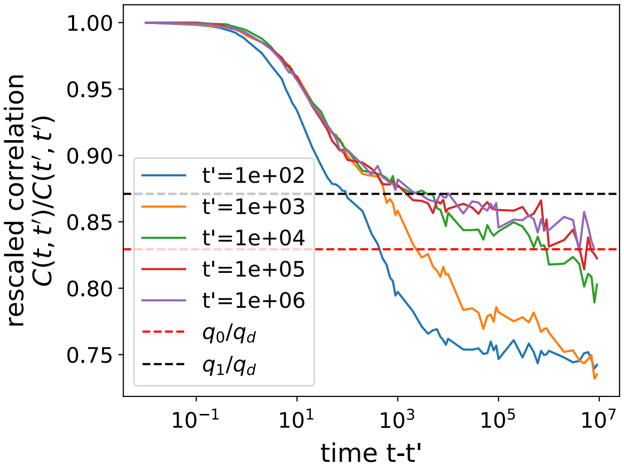

FIG. 4. Rescaled correlation as a function of $(t - t')$, for different age t' of the system, showing aging dynamics. The dashed black and red lines correspond respectively to the theoretical predictions for q_1 and q_0, both rescaled by the analytical prediction $C(t', t') \equiv q_d$.

$$\forall\, t \geq t' > t_{\mathrm{wait}} \quad \mathbb{E}[N(t)N(t')] = C(t, t') \simeq C(t - t'). \tag{7}$$

This convergence to a time translationally invariant regime is shown in Fig. 3. The long-time limit of $C(t - t')$ is the overlap between two generic configurations belonging to the single equilibrium state: the dashed line in Fig. 3 is the analytical prediction for $\lim_{t-t'\to\infty} C(t - t')$, which is in perfect agreement with the numerics. We have also checked that this agreement holds upon varying T, and for other observables the results are reported in the SM, Section V. D (see Fig. 6). From the time dependence of $C(t - t')$, one can estimate the typical timescale characterizing dynamical fluctuations within the single equilibrium phase. Formally, we define τ_{decorrel} by the identity

$$\frac{C(\tau_{\mathrm{decorrel}}) - C(\infty)}{[C(0) - C(\infty)]} = 0.3, \tag{8}$$

where 0.3 is an arbitrary value set for the sake of the definition. In Fig. 3, we also plot τ_{decorrel} as a function of $(T - T_{1\mathrm{RSB}})$, where $T_{1\mathrm{RSB}}$ is the critical value of T at which the single equilibrium phase becomes unstable (blue line in Fig. 1). We find that the thermodynamic instability is accompanied by a dynamical transition at which τ_{decorrel} diverges as a power law with an exponent close to 0.5 (see the inset plot of Fig. 3).

For small demographic noise, i.e., when T is below the blue line of Fig. 1, previous results on the dynamics of mean-field spin glasses [74–76] suggest that the LV model should never reach an equilibrium stationary state; instead it should display "aging" [77,78]. In fact, one expects that, among the very many equilibria, the dynamics starting from high-temperature-like initial conditions falls in the basin of attraction of the most numerous and marginally stable equilibria and displays aging behavior. This is indeed what we report in Fig. 4, which shows that the older the system is, the longer it takes to decorrelate. The landscape interpretation of this phenomenon is that the system approaches at long times a part of configuration space with many marginally stable equilibria. This leads to aging because the longer the time, the smaller the fraction of unstable directions to move, hence the slowing down of the dynamics. The exploration never stops, however, and eventually the system never settles down in any equilibrium [79–81]. The two dashed lines in Fig. 4 correspond to our analytical prediction for the intrastate and the interstate overlaps of the marginally stable equilibria. The agreement is satisfactory, but larger times would be needed to fully confirm it.

Our characterization of the phases and the dynamics of the LV model has important consequences for related systems, in particular the so-called random replicant models (RRMs), which consist of an ensemble of replicants evolving according to random interactions. Given their numerous applications in biology, optimization problems [34,82], and evolutionary game theory [83,84], RRMs still attract great theoretical interest. The RRM, which was introduced in [34] and further studied in [38], is remarkably similar to the disordered LV model we studied. In the case of symmetric interactions, one can map the RRM problem onto a model described by the following Hamiltonian:

$$H_R = -\sum_{i<j=1}^{S} J_{ij} x_i x_j - a \sum_{i=1}^{S} x_i^2, \tag{9}$$

where x_i/S is the concentration of the ith family in the species pool subject to the global constraint $\sum_i x_i = S$ for all $x_i \geq 0$. The couplings J_{ij} are independent identically distributed Gaussian variables with variance J^2/S. With an appropriate rescaling of the interaction matrix, we can show that the average interaction term μ for LV plays the same role as the Lagrange multiplier, which is introduced in the RRM to enforce the sum of all concentrations to be fixed. The main difference with respect to Eq. (4) is the absence of the logarithmic term. Our analysis can be fully extended to the RRM, as we show in the SM, Section III. The main result is that the three phases we found for the LV model are present also for the RRM and organized in a phase diagram (see Fig. 4 in the SM) that is remarkably similar to the one in Fig. 1. This strengthens the generality of our results and clarifies the nature of the glassy phase of the RRM that was first investigated in [38].

Let us finally discuss how we expect our results to change if the interactions contain a small random asymmetric component. The multiple-basins structure associated with the 1RSB phase should not be affected because its basins correspond to stable stationary states, and a small nonconservative random force should not destabilize them [85]. On the contrary, the fractal structure (characteristic of the Gardner phase) and the decomposition into sub-basins are expected to be wiped out because of the marginal stability of the equilibria associated with it [32,46,47]. In the absence of demographic noise, one therefore expects a single equilibrium at small σ, which is replaced by an exponential number of chaotic attractors at large σ. The demographic noise adds additional dynamical fluctuations to these multiple equilibria and eventually makes them merge in a single one, thus leading to a phase diagram similar to Fig. 1 but with only the blue line and two phases (single and multiple equilibria).

In conclusion, we have unveiled a complex and rich structure for the organization of equilibria in a central model for ecological communities. Our results, supported by dynamic simulations, highlight the relevance of multiple equilibria phases for the dynamics of many strongly interacting species for which one can also imagine reproducing controlled, experimental setups [63,86,87]. Moreover, our findings clarify the glassy nature of the equilibria previously studied in [5,19,20,22,88]. As we have shown, our results carry out to more general contexts, and we expect they will be directly relevant for evolutionary game theory models such as the ones discussed in [89]. Extensions to go beyond the well-mixed assumption and to include space effects are certainly worthy of future investigations [90].

We expect that the collective dynamical behaviors—the phases—found in this work go beyond the LV model itself and may play an important role in a variety of contexts from biology to economics, which can be modeled by high-dimensional dynamical systems with random couplings.

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[42] See Supplemental Material, which includes Refs. [19,20,22,34,39,42,44–62], at http://link.aps.org/supplemental/10.1103/PhysRevLett.126.258301 for a detailed description of the analytical solution, which has been obtained in both the single-equilibrium and multiple-equilibrium phases, along with the computation of the configurational entropy in this second case. The second part of the SM focuses on the numerical techniques used to solve the dynamical equations and appropriately take the demographic noise into account.

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