

Stabilization of macroscopic dynamics by fine-grained disorder in many-species ecosystems

Juan Giral Martínez¹, Silvia De Monte^{1,2,*} and Matthieu Barbier^{3,4,5,*}

¹*Institut de Biologie de l'École Normale Supérieure, Département de Biologie, École Normale Supérieure, PSL Research University, Paris, France*

²*Max Planck Institute of Evolutionary Biology, Plön, Germany*

³*CIRAD, UMR PHIM, 34090 Montpellier, France*

⁴*PHIM Plant Health Institute, University of Montpellier, CIRAD, INRAE, Institut Agro, IRD, 34090 Montpellier, France*

⁵*Institut Natura e Teoria en Pirenèus, Surba, France*



(Received 10 December 2024; revised 7 March 2025; accepted 14 July 2025; published 4 September 2025)

Models for complex, heterogeneous systems such as ecological communities vary in the level of organization they describe. When the dynamics at the species level is unknown, one typically resorts to heuristic "macroscopic" models that capture relationships among a few degrees of freedom, e.g., groups of similar species, and commonly display out-of-equilibrium dynamics. These models, however, exactly reflect the species-level "microscopic" dynamics only when microscopic heterogeneity can be neglected. Here, we address the robustness of such macroscopic descriptions to the addition of disordered microscopic interactions. While disorder is known to destabilize equilibria at the microscopic level, leading to asynchronous (typically chaotic) fluctuations, we show that it can also stabilize synchronous species fluctuations driven by macroscopic structure. We analytically find the conditions for the existence of heterogeneity-stabilized equilibria and relate their stability to a mismatch in the time scales of individual species. This may shed light on the empirical observation that many-species ecosystems often appear stable despite highly diverse and potentially destabilizing interactions between species and functional groups.

DOI: [10.1103/PhysRevE.112.034305](https://doi.org/10.1103/PhysRevE.112.034305)

I. INTRODUCTION

Complex systems encompass different levels of description, but interest is often focused on system-level properties that integrate out microscopic details [1]. Classical ecosystem models, for instance, heuristically describe the dynamics of communities in terms of a few functionally distinct groups [2–4] (e.g., phytoplankton and zooplankton; producers, consumers, and decomposers, etc.), treating the numerous species that compose them as equivalent [5]. In such low-dimensional population models, system-level dynamics is not derived by coarse-graining microscopic degrees of freedom. Therefore, their conclusions are not guaranteed to be robust when microscopic heterogeneity among species is added [6].

On the contrary, high-dimensional models, such as the random generalized Lotka-Volterra equations (rGLV) [7,8], start from defining the microscopic dynamics of every species. There, microscopic parameter heterogeneity generically destabilizes equilibria. The loss of microscopic stability has been analytically characterized, via random matrix theory, as a disorder-induced phase transition [9]. Even when single species abundances fluctuate, however, they average out at the

community level [10–12], so that this transition does not manifest when one looks at macroscopic, aggregated variables.

In this Letter, we consider the effects of adding heterogeneity to a system that, like many low-dimensional ecological models [13–15], is macroscopically out-of-equilibrium. The Lotka-Volterra equations provide a simple representation of nonlinear interactions between G macroscopic degrees of freedom (the groups of species). Accordingly, the total abundance N_α , $\alpha = 1, \dots, G$ of species belonging to group α obeys

$$\frac{dN_\alpha}{dt} = r_\alpha N_\alpha \left(1 - N_\alpha - \sum_{\beta=1}^G M_{\alpha\beta} N_\beta \right) + \theta, \quad (1)$$

where r_α and $M_{\alpha\beta}$ quantify the intrinsic growth rate of single groups and the interaction between pairs of groups, respectively, and $\theta \ll 1$ models the migration from outside the community. In this representation, differences between species are neglected, so that single species have exactly the same dynamics as their group.

In real systems, however, group dynamics results from the aggregation of the abundance of many diverse species. We therefore consider that each group is composed of a large number S_g of species (for a total of $S = GS_g$ species in the community), whose interactions are random perturbations of their group's interactions. In such a high-dimensional model, the abundance x_i of a species belonging to group α , and with

*These authors contributed equally to this work.

intrinsic growth rate r_i obeys

$$\frac{dx_i}{dt} = r_i x_i \left(1 - x_i - \sum_{j=1}^S A_{ij} x_j \right) + \theta. \quad (2)$$

The effect of species j in group β on the growth of species i is $A_{ij} = \mu_{ij}/S_g + \sigma \xi_{ij}/\sqrt{S}$, where $\mu_{ij} = M_{\alpha\beta}$ and ξ_{ij} are independent random variables with zero mean and unit variance (which reduces to the rGLV when $G = 1$ and thus $\mu_{ij} = \mu$ [8,10]). We discuss below the properties of this interaction matrix, where the strength of group-level interactions (responsible for the low-rank matrix structure) relative to disorder is controlled by the heterogeneity parameter σ .

The low- and high-dimensional models can be compared by looking at the mean abundance of the species belonging to one group $m_\alpha(t) = S_g^{-1} \sum_{i \in \alpha} x_i(t)$. For $\sigma = 0$, the scaling of Eq. (2) with S_g implies that species interact only through $m_\alpha(t)$. In particular, species within a group have identical equations and synchronize after a transient. Asymptotically, both species and groups thus follow the same dynamics as the low-dimensional model, i.e., $m_\alpha(t) = N_\alpha(t)$.

II. PHENOMENOLOGY AND PHASE DIAGRAM

We address the effect of increasing σ when such dynamics are out of equilibrium. Consider, for instance, a community composed of three groups with rock-paper-scissors (RPS) interactions

$$M = \begin{pmatrix} 0.5 & \kappa & 0 \\ 0 & 0.5 & \kappa \\ \kappa & 0 & 0.5 \end{pmatrix}, \quad (3)$$

identical growth rates $r_\alpha = 1$, and a small immigration rate $0 < \theta \ll 1$. Group dynamics only depend on the strength κ of competition between pairs of groups: at $\kappa = 3$ a Hopf bifurcation marks the transition from equilibrium coexistence at $N_\alpha^*(\kappa) = 1/(1.5 + \kappa)$ to limit-cycle oscillations.

The high-dimensional model, on the other hand, possesses three meaningful phases, which depend, beside κ , on heterogeneity σ (Fig. 1). In the fixed point phase (FP), both species and group abundances converge to a unique and stable fixed point, where all groups coexist (though some species may go extinct), see Fig. 2(c). In the synchronous oscillations (SO) phase, species fluctuate coherently with the mean abundance $m_\alpha(t)$ of their group [Fig. 2(a)]. Upon increasing σ in this phase, species remain synchronized. Heterogeneity of parameters among species, however, modifies the shape of their trajectory, spreading out the phase and amplitude of the oscillations [Fig. 2(b)]. In the asynchronous fluctuations phase (AF), incoherent species oscillations manifest, at the group level, in irregular fluctuations of $m_\alpha(t)$ that disappear in the limit of large S [7]. The transition FP/AF results in the emergence of chaotic dynamics at the species level, akin to the disorder-induced instability of the rGLV [10,16–18]. The other two transitions—FP/SO and SO/AF—are specific to our system and reflect the interplay between macroscopic structure and microscopic disorder.

A linear stability analysis around the equilibrium of the FP phase allows us to analytically characterize the FP/AF and FP/SO transitions. Equilibrium abundances can be ob-

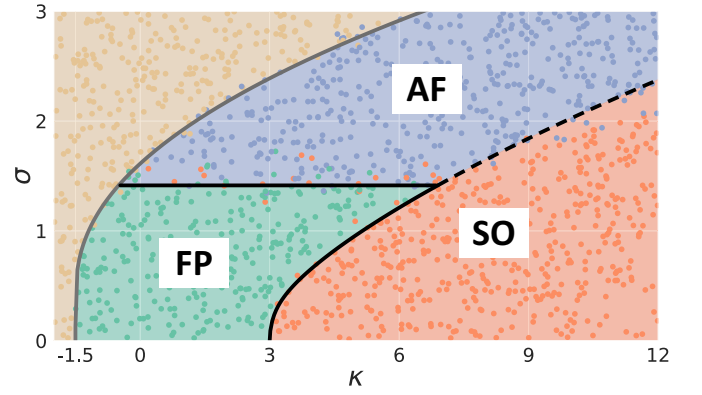


FIG. 1. Phase diagram of the microscopic RPS, displaying the three meaningful phases described in the text (SO in orange, FP in green, and AF in blue), as well as the physically unrealistic unbounded growth phase (yellow) [10]. Points are numerical simulations for particular realizations of disorder in groups of size $S_g = 500$, and their color reflects the qualitative dynamics as classified through the analysis of species abundance time series (see Appendix B). Lines and background colors are analytical predictions. The SO/FP transition line was obtained using Eq. (7). The FP/AF transition and the divergent transition (gray line) are the same as in [10,11] up to the substitution $\mu = \tilde{\kappa}$ (see Appendix D). While our analysis does not apply to the SO/AF transition, a calculation assuming the fixed point solution in the blue phase yields a reasonable approximation (dashed line).

tained by dynamical mean field theory (DMFT) [7,11], which establishes an equivalence between the coupled dynamics with quenched randomness of Eq. (2) and a set of uncoupled stochastic processes. In Appendix C, we show that the dynamics possesses a single stable fixed point, where all groups coexist symmetrically, i.e., $m_1 = m_2 = m_3 \equiv m(\kappa, \sigma)$. For $\sigma = 0$, every species has the same equilibrium of the low-dimensional system $x_i^* = N_\alpha^*(\kappa)$. For $\sigma > 0$, instead, we show that species abundances are distributed as the truncated Gaussian

$$x_i^* = (1 - \tilde{\kappa}m) \max(0, 1 + \sqrt{\eta} \zeta_i), \quad (4)$$

where $\tilde{\kappa} = \kappa + 1/2$, ζ_i are independent standard Gaussian variables and $\eta = \sigma^2 q / (1 - \tilde{\kappa}m)^2$, with $q = S^{-1} \sum_i \langle (x_i)^2 \rangle$, is the spread in species abundances. The equilibrium macroscopic parameters m, η satisfy closed-form equations [see Eq. (C8)], whose solution indicates that η is an increasing function of heterogeneity σ .

III. DISORDER-INDUCED STABILIZATION OF MACROSCOPIC DYNAMICS

We now linearize the dynamics Eq. (2) around the fixed point given by Eq. (4). Let $\delta x_i(t) = x_i(t) - x_i^*$ be a perturbation to the abundances of extant species. Through DMFT, their dynamics can be equivalently described (see Appendix D) by the linear stochastic process

$$\frac{d}{dt} \delta x_i = r_i x_i^* \left(-\delta x_i - \sum_{\beta} M_{\alpha\beta} \delta m_{\beta} + \sigma \delta \zeta_i \right), \quad (5)$$

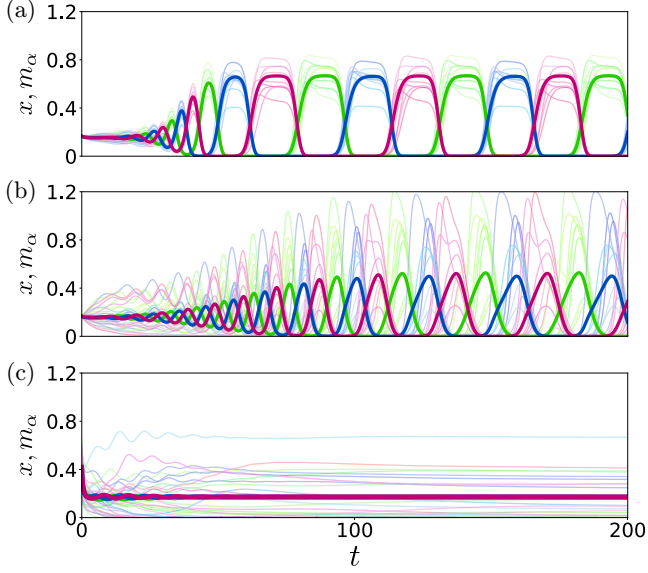


FIG. 2. Trajectories for the microscopic RPS system in the SO phase. Thin lines are a subset of species's trajectories, color coded as the groups they belong to, whose average abundance is represented as thick lines. As heterogeneity increases from $\sigma = 0.25$ (a) to 0.75 (b), synchronous trajectories become less coherent, the amplitude of the group oscillations decreases and the transient becomes longer. Finally, the system develops a stable fixed point, seen here at $\sigma = 1.1$ (c). In this simulation, $\kappa = 5$ and $S_g = 300$.

where $\delta\zeta_i$ are independent, centered Gaussian processes. We have also defined $\delta m_\beta(t) = S_g^{-1} \sum_{i \in \beta} \langle \delta x_i(t) \rangle_{x^*}$, where the average is taken with respect to the stochastic process Eq. (5), given the fixed point abundances x^* . We characterize such a stochastic process through its first two moments. In Appendix D, we show how the FP/AF transition corresponds to the divergence of the second moment and occurs, in a class of models including the RPS (discussed later), when $\sigma = \sqrt{2}$, as in the rGLV [19].

In the remaining of this Letter, we focus on the first moments $\langle \delta x_i(t) \rangle_{x^*}$ when the second moments do not diverge. In the FP and AF phases, where the dynamics are either stable or asynchronous, $\langle \delta x_i(t) \rangle_{x^*}$ vanish as $t \rightarrow \infty$. They instead remain finite when synchronous oscillations emerge at the FP/SO transition. Averaging Eq. (5) yields an $S \times S$ linear system (see Appendix D),

$$\frac{d}{dt} \langle \delta x_i \rangle = (1 - \tilde{\kappa}m) \sum_j \mathcal{J}_{ij} \langle \delta x_j \rangle, \quad (6)$$

where we have defined $\mathcal{J}_{ij} = -z_i^*(\delta_{ij} + S_g^{-1}\mu_{ij})$, and, for mathematical convenience, the rescaled abundances $z_i^* = r_i x_i^* / (1 - \tilde{\kappa}m)$. In the following, we refer to $\mathcal{J}$ as the pseudo-Jacobian matrix. Indeed, it resembles the Jacobian of Eq. (2), $J_{ij} = -r_i x_i^*(\delta_{ij} + A_{ij})$, evaluated over extant species, but does not feature the disordered component. The spectrum of $\mathcal{J}$, as most random matrices, contains a bulk of eigenvalues and a few outliers [Fig. 3(b)]. The bulk diagonal is marginally stable but uninformative, and stability depends instead on the real part of the outliers.

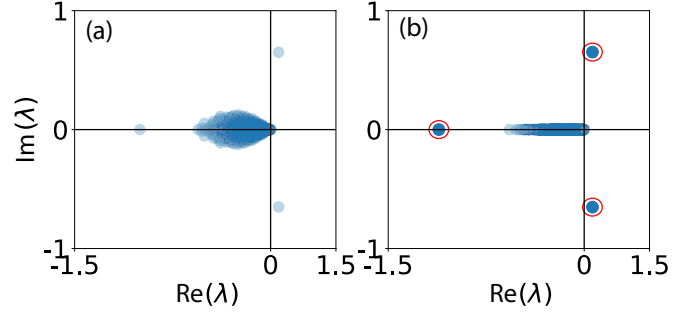


FIG. 3. Spectrum of the Lotka-Volterra Jacobian J (a) and the pseudo-Jacobian $\mathcal{J}$ (b) for the RPS system with parameters $\kappa = 5$ and $\sigma = 0.75$. The red circles are predictions using Woodbury's identity Eq. (7). On top of such outliers, the pseudo-Jacobian features a bulk of stable eigenvalues, corresponding to its diagonal component.

For $\sigma = 0$, the outliers of $\mathcal{J}$ are, up to a rescaling, the eigenvalues of the Jacobian of the low-dimensional system, given by $J_{\alpha\beta}^M = -r_\alpha N_\alpha (\delta_{\alpha\beta} + M_{\alpha\beta})$, hence the stability of the high- and low-dimensional systems is the same. As σ is increased, each outlier λ_0 is continuously modified into an outlier $\lambda(\sigma)$ of $\mathcal{J}$, which depends on disorder exclusively through the distribution of z_i^* . For the RPS system, $\lambda(\sigma)$ is related to $\lambda_0 = (3 - \kappa \pm i\kappa\sqrt{3})/2$ by

$$\phi(\sigma) \left\langle \frac{1 + \lambda_0}{1 + z^{-1}\lambda(\sigma)} \right\rangle_{z>0} = 1, \quad (7)$$

where $\phi(\sigma)$ is the fraction of surviving species and the average is realized on extant species (see Appendix E). By combining Eq. (7) with the equilibrium distribution Eq. (4) and by solving $\text{Re } \lambda(\sigma) = 0$, we obtain an analytical expression for the line $\sigma(\kappa)$ identifying the FP/SO transition in Fig. 1.

The first term of Eq. (7) captures the effect of extinctions on stability. Upon increasing σ , $\phi(\sigma)$ decreases and this results in a reduction of $\text{Re } \lambda(\sigma)$. Hence, disorder first stabilizes through extinctions. Indeed, species in smaller communities tend to experience weaker competition. This trivial effect can however be compensated by scaling the interactions by ϕS . The second term captures the dependence on equilibrium abundances. Disorder acts on this term by increasing the spread of z_i^* . This effect is independent of extinctions. In order to focus on how $\lambda(\sigma)$ varies with such increase in abundance heterogeneity, we drop the dependency of Eq. (7) on ϕ and differentiate with respect to σ (see Appendix E), yielding

$$\frac{1}{\eta'(\sigma)} \frac{d\lambda}{d\sigma} = -\lambda \int_0^\infty \frac{\rho_\eta(\sigma)(z) dz}{(\lambda + z)^3} \left(\int_0^\infty \frac{\rho_\eta(\sigma)(z) z dz}{(\lambda + z)^2} \right)^{-1} \quad (8)$$

where $\rho_\eta(z) = (2\pi\eta)^{-1/2} \exp(-(z-1)^2/2\eta)$ is the distribution of z^* , obtained from Eq. (4). For real and positive eigenvalues, the integrals are positive. Thus, λ decreases with σ , converging to 0^+ for large heterogeneity, and never crosses the imaginary axis. The real part of complex eigenvalues, on the other hand, can become negative. Plotting the flow associated to the r.h.s. of Eq. (8) in Fig. 4 allows us to understand how λ changes as σ grows. Any initially unstable λ_0 moves leftwards, and eventually crosses the imaginary axis through a Hopf bifurcation. The blue lines illustrate how two outlier

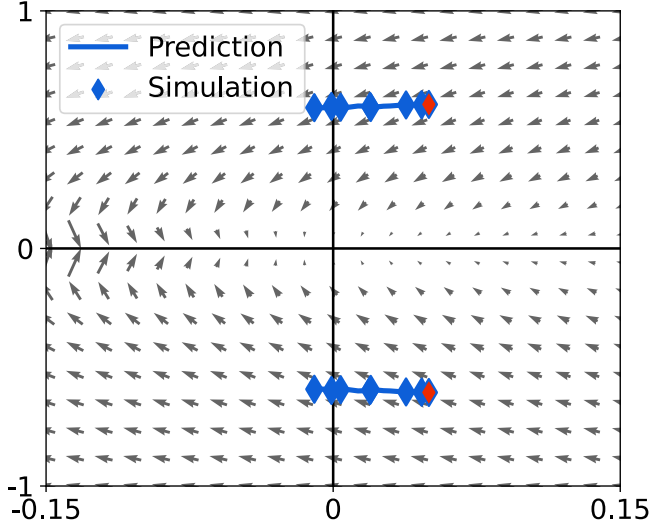


FIG. 4. Flow of eigenvalues for the RPS system, as predicted by Eq. (8) (arrows). Starting from λ_0 (red diamond), the real part of the eigenvalue $\lambda(\sigma)$ moves leftwards as disorder increases, thus enhancing stability. The blue line shows a prediction based on Eq. (7) for its trajectory between $\sigma = 0$ and $\sigma = 0.5$, for $\kappa = 3.5$. It displays an excellent agreement with numerical simulations for $S_g = 300$ (diamonds), where the abundance distribution was obtained by numerically solving the equilibrium of Eq. (2) and then calculating the eigenvalues of the $S \times S$ matrix $\mathcal{J}$. Given that the r.h.s. of Eq. (8) depends on σ , the vector field in general changes with the intensity of disorder, and is here depicted for $\sigma = 0$.

eigenvalues of an initially oscillating system get stabilized when σ varies between 0 and 0.5.

The suppression of oscillations hence occurs, even in the absence of species extinctions, by a disorder-induced spread in (positive) equilibrium abundances Eq. (4). According to the definition of $\mathcal{J}$, these set the "intrinsic" time scales of species i around the fixed point. Despite such time scales becoming mismatched, the existence of macroscopic oscillations implies that species within the same group are locked to the same frequency. Increasing microscopic heterogeneity then results in the spreading out of their oscillatory trajectories, with species booming sooner or later, depending on their parameters [see Fig. 2(b)]. The consequent dephasing decreases, in turn, the amplitude of $m_\alpha(t)$ and, eventually, stamps out oscillations at both the microscopic and the macroscopic scales. Ultimately, stabilization is a consequence of the multiplicative nature of ecological equations, defined in terms of per capita demographic rates—so that abundance directly sets the time scale of species variation. The same principle also applies to other sources of microscopic disorder, for instance heterogeneity in the intrinsic growth rates r_i , which appear in combination to x_i^* in defining $\mathcal{J}$.

The synchronicity of the FP/SO transition recalls amplitude death, which occurs in populations of strongly coupled oscillators when the mismatch of intrinsic frequencies is increased [20–24]. In our system, however, the oscillation of microscopic variables is due to the feedback with the macroscopic level, instead of being intrinsic. Moreover, for intermediate σ , single species oscillations are qualitatively

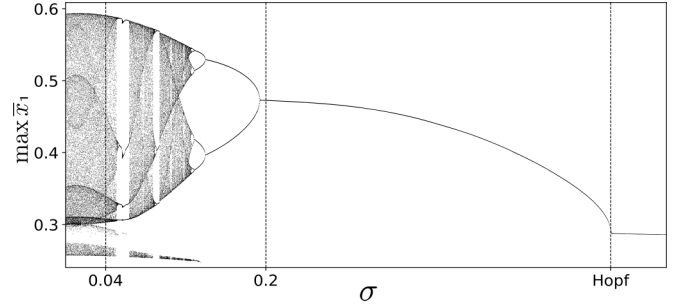


FIG. 5. Poincaré map of a system with chaotic macroscopic dynamics (Appendix A) when changing heterogeneity, obtained by numerical integration of Eq. (2). For small σ (e.g., $\sigma = 0.04$), both the microscopic and macroscopic systems have chaotic dynamics. Chaos is lost through an inverse Feigenbaum cascade, it becomes cyclic (e.g., $\sigma = 0.2$), and ultimately reaches a fixed point through a Hopf bifurcation.

different than both those of the group average and of the disorderless equations.

Disorder-induced stabilization can be generalized beyond the illustrative RPS example. Indeed, the calculations leading to Eq. (7) are valid whenever growth rates r_i and distributions of species abundances Eq. (4) are group independent. Such group-symmetric fixed points are, in fact, found in any system such that $\vec{1}$ is an eigenvector of μ (see Appendix C). Their stability is obtained by replacing $\tilde{\kappa}$ with its associated eigenvalue (see Appendix E). Furthermore, given that Eq. (8) does not depend on $\tilde{\kappa}$, the flow of Fig. 4 is unchanged and disorder always acts toward stabilizing the group dynamics. If such a symmetry does not hold and the equilibrium species distributions differ between groups, the stability of fixed points can still be assessed using Eq. (E2), but no simple criterion seems to define when the resulting flow is stabilizing. Nonetheless, numerical simulations with different matrices M indicate that out-of-equilibrium macroscopic regimes are often stabilized by heterogeneity.

Disorder, moreover, appears to cause bifurcations between dynamical attractors other than fixed points, so that linear stability should not in principle be relevant. As an example, consider a macroscopic system composed of four chaotically oscillating groups [13], whose interaction matrix and growth rates are given in Appendix A. Increasing σ in the microscopic model makes the oscillations undergo an inverse Feigenbaum cascade (Fig. 5), where chaos is lost through a sequence of period-halving bifurcations, eventually leading to a Hopf bifurcation. The ability of microscopic heterogeneity to stabilize the community dynamics may be again connected to the spreading of time scales, even far from equilibria [24], but this point requires further investigation.

IV. DISCUSSION

Low-dimensional models that describe the effects of nonlinearities on macroscopic observables, like heuristic models commonly used in ecology and other complex systems, are exact only if all microscopic degrees of freedom are identical. In this Letter, we made explicit the microscopic underpinning of low-dimensional macroscopic equations, and addressed

the effect of fine-grained heterogeneity on the dynamics. We unveiled a tension between microscopic disorder that makes species dynamics different from one another, and macroscopic structure, which keeps the synchrony of out-of-equilibrium fluctuations. This tension can lead to bifurcations between different regimes, including the suppression of macroscopic oscillations.

The change of fixed point stability is the simplest such bifurcation. We have shown that quenched disorder results in a mismatch in the intrinsic timescales of the microscopic degrees of freedom. As the microscopic dynamics become less coherent, the amplitude of macroscopic fluctuations decreases. While we have only characterized such transition for group-symmetric systems, numerical simulations show that the phenomenon is more general. In particular, stabilization can involve transitions between out-of-equilibrium regimes reminiscent of the bifurcation cascades observed for low-dimensional dynamical systems. The exploration of such transitions is an interesting future avenue of investigation. Similarly, future work should address how the SO/AF transition stems from an interference between the macroscopic dynamics and the invasion-extinction dynamics explored in [17,25]. Finally, we expect our results to be relevant whenever multiplicative growth is posited, such as in economics [26].

This study raises a fundamental question: what is the scale of aggregation most relevant for addressing stability? Indeed, disorder has long been known to have a destabilizing effect on microscopic dynamics [9]. This manifests here as the FP/AF transition where, however, microscopic dynamics are asynchronous and do not generate macroscopic fluctuations. Thus, transitions that involve the macroscopic dynamics require a certain degree of synchronization, and are stabilized by the mechanism we unveiled. This is particularly relevant in ecology. When the functioning and resilience of an ecological community depends on the stability of a few macroscopic observables such as the abundance of functional groups [1], our model suggests that fine-grained heterogeneity could make communities more robust. On the contrary, we expect ecosystems whose function depends on a small set of species (so-called "keystone" [27]) to be fragile to heterogeneity-induced extinctions.

Recently, high-throughput methods for acquiring data on ecological and especially microbial communities have revealed ubiquitous fluctuations and heterogeneity at species and subspecies levels [28–31]. Yet, more macroscopic descriptions, based on large taxonomic groups or ecological functions, are markedly stable across systems [2,32–34] and over time [35,36]. Classical explanations for ecosystem-level stability invoked asynchronicity of species fluctuations [37,38]. Our model suggests that they may also stem from species heterogeneity within strongly interacting functional groups, which would result in the concomitant stabilization of both levels.

More generally, in order to understand the dynamics of a complex system, it is useful to discern its behavior at different levels of description simultaneously. While this may be difficult in many practical situations, microbial communities—where the dynamics can be assessed at the level of functional groups, but also down to the strain level

[39,40]—offer a particularly attractive opportunity for determining what kind of heterogeneity-induced transitions are most pertinent to real systems.

ACKNOWLEDGMENTS

We thank Guy Bunin and Jean-François Arnoldi for inspiration and discussions, and Emil Mallmin for sharing his code. J.G.M. acknowledges the support of the Frontiers in Innovation, Research and Education program. S.D.M. was supported by the French Government under the program Investissements d'Avenir (ANR-10-LABX-54 MEMOLIFE and ANR-11-IDEX-0001-02PSL). This research was co-funded by the European Union (Grant Agreement No. 101059915 - BIOcean5D).

APPENDIX A: PARAMETERS OF THE CHAOTIC MODEL

The matrix M and the growth rates for the low-dimensional chaotic system are

$$r = \begin{pmatrix} 1 \\ 0.72 \\ 1.53 \\ 1.27 \end{pmatrix}, \quad M = \begin{pmatrix} 0 & 1.09 & 1.52 & 0 \\ 0 & 0 & 0.44 & 1.36 \\ 2.33 & 0 & 0 & 0.47 \\ 1.21 & 0.51 & 0.35 & 0 \end{pmatrix}. \quad (\text{A1})$$

Like in the RPS case, the high-dimensional model is obtained by dividing each group into S_g species and adding a disordered component to the interactions. We introduce no heterogeneity in the r_i when building the high-dimensional model, that is $r_i = r_\alpha$ for any i in group α .

APPENDIX B: NUMERICAL SIMULATIONS

All numerical simulations were performed using Python's `solve_ivp` function during a time interval T . The immigration rate was set to $\theta = 10^{-8}$. We classified the trajectories in Fig. 1 as follows:

(i) Trajectories for which the solver stops before T are classified as divergent. Indeed in this case the divergence occurs in finite time and the solver fails.

(ii) For nondivergent trajectories, we considered the temporal variance, averaged over species: $S^{-1} \sum_i \langle x_i^2 \rangle_T - \langle x_i \rangle_T^2$. Simulations for which this variance is smaller than $10^{-2}/\sqrt{T}$ were classified as UFP.

(iii) For trajectories that are neither divergent nor UFP, we considered the peaks of the power spectrum $|\hat{m}_\alpha(\omega)|^2$ of group abundances. Trajectories for which such peaks followed an arithmetic progression (as expected for periodic motion) were classified as SO. Otherwise we classified them as AF.

APPENDIX C: OBTAINING THE ABUNDANCE DISTRIBUTION

The evolution equation for species i in group α can be written

$$\frac{dx_i}{dt} = r_i x_i \left(1 - x_i - \sum_\beta M_{\alpha\beta} m_\beta(t) - \frac{\sigma}{\sqrt{S}} \sum_j \xi_{ij} x_j \right) + \theta, \quad (\text{C1})$$

where we have introduced the group abundances $m_\alpha(t) = S_g^{-1} \sum_{j \in \alpha} x_j(t)$. The well-established framework of dynamical mean field theory [7,16,41] can be used to replace the random term in this equation by an effective Gaussian noise correlated in time, when the number of species is large $S \gg 1$. Here, we derive DMFT using the cavity method [7], which assumes that the dynamics of species i can be understood from its perturbative effect on the dynamics of the rest of the community.

Let $x_j^\backslash(t)$ be the dynamics of species j in the absence of species i . Upon adding species i , we assume a small perturbation of the form,

$$x_j(t) = x_j^\backslash(t) - \sum_{k \neq i} \int_0^t ds G_{jk}(t, s) A_{ki} x_i(s), \quad (\text{C2})$$

where $G_{jk}(t, s)$ is the linear response of species j at time t with respect to species k at time $s < t$. Plugging this in the equation for i yields

$$\begin{aligned} \frac{dx_i}{dt} = & r_i x_i \left(1 - x_i - \sum_{\beta} M_{\alpha\beta} m_{\beta} - \frac{\sigma}{\sqrt{S}} \sum_j \xi_{ij} x_j^\backslash(t) \right) \\ & + \frac{1}{S} \sum_{j, k \neq i} \xi_{ij} \xi_{ki} \int_0^t ds G_{jk}(t, s) x_i(s). \end{aligned} \quad (\text{C3})$$

In the first line, the $x_j^\backslash(t)$ are by definition independent of ξ_{ij} . Thus, the central limit theorem applies and this term converges, for $S \rightarrow \infty$, to a Gaussian process with mean zero and correlator $S^{-1} \sum_j \langle x_j(t) x_j(s) \rangle$. In the second line, $G_{jk} \sim 1/\sqrt{S}$ for off-diagonal terms and ~ 1 for diagonal ones. Furthermore, $\langle \xi_{ij} \xi_{ki} \rangle = 0$ for all terms. Hence, the second line averages out, and one obtains an effective SDE for each species,

$$\frac{dx_i}{dt} = r_i x_i \left(1 - x_i - \sum_{\beta} M_{\alpha\beta} m_{\beta}(t) + \sigma \zeta_i(t) \right) + \theta, \quad (\text{C4})$$

where ζ_i are Gaussian processes with zero mean and correlation $\langle \zeta_i(t) \zeta_j(s) \rangle = \delta_{ij} S^{-1} \sum_k \langle x_k(t) x_k(s) \rangle$. The averages are w.r.t. the stochastic processes in Eq. (C4). In particular, the m_α appear as averages over a large number of independent processes, and are thus deterministic processes. Setting Eq. (C4) at equilibrium and using $\theta \ll 1$ we obtain

$$x_i = 0 \quad \text{or} \quad x_i = 1 - \sum_{\beta} M_{\alpha\beta} m_{\beta} + \sigma \zeta_i. \quad (\text{C5})$$

In order for the equilibrium to be stable, extinct species must have a negative growth rate (otherwise they could invade). This condition must be satisfied by setting

$$x_i^* = \max \left(0, 1 - \sum_{\beta} M_{\alpha\beta} m_{\beta} + \sigma \zeta_i \right). \quad (\text{C6})$$

We can then self-consistently use Eq. (C6) to calculate $q = S^{-1} \sum_i \langle x_i^2 \rangle$ and $m_\alpha = S_g^{-1} \sum_{i \in \alpha} \langle x_i \rangle$,

$$m_\alpha = \sigma \sqrt{q} \omega_1 \left(\frac{1 - \sum_{\beta} M_{\alpha\beta} m_{\beta}}{\sigma \sqrt{q}} \right)$$

$$1 = \sigma^2 G^{-1} \sum_{\alpha} \omega_2 \left(\frac{1 - \sum_{\beta} M_{\alpha\beta} m_{\beta}}{\sigma \sqrt{q}} \right), \quad (\text{C7})$$

with $\omega_k(s) = (2\pi)^{-1/2} \int_{-1/\sqrt{s}}^{\infty} \exp(-z^2/2) (z + 1/\sqrt{s})^k dz$. For matrices M having $\vec{1}$ as an eigenvector with eigenvalue $\tilde{\kappa}$, these equations have a solution where all groups have the same mean abundance. This is the case of the RPS system with $\tilde{\kappa} = \kappa + 1/2$. Indeed, setting $m_\alpha = m$ in Eq. (C7) yields

$$\begin{aligned} m &= \sigma \sqrt{q} \omega_1 \left(\frac{1 - \tilde{\kappa} m}{\sigma \sqrt{q}} \right) = \sigma \sqrt{q} \omega_1 \left(\frac{1}{\sqrt{\eta}} \right) \\ 1 &= \sigma^2 \omega_2 \left(\frac{1 - \tilde{\kappa} m}{\sigma \sqrt{q}} \right) = \sigma^2 \omega_2 \left(\frac{1}{\sqrt{\eta}} \right), \end{aligned} \quad (\text{C8})$$

where η is defined in the main text. In particular, ω_2 is increasing, and so $\eta(\sigma)$ is also increasing. Furthermore, the group structure also disappears from Eq. (C6), and we obtain Eq. (4) in the main text. For the RPS, this turns out to be the only possibly stable equilibrium. This is because solutions with only one group remaining can always be invaded by another one, while solutions with two groups are such that one excludes the other.

APPENDIX D: STABILITY CONDITIONS

Linear stability can be assessed from the effective process Eq. (C4). Let $\delta x_i(t) = x_i(t) - x_i^*$ be a small perturbation to the fixed point abundances. To first order,

$$\begin{aligned} \frac{d}{dt} \delta x_i = & r_i \delta x_i \left(1 - x_i^* - \sum_{\beta} M_{\alpha\beta} m_{\beta} + \sigma \zeta_i \right) \\ & + r_i x_i^* \left(-\delta x_i - \sum_{\beta} M_{\alpha\beta} \delta m_{\beta} + \sigma \delta \zeta_i \right). \end{aligned} \quad (\text{D1})$$

Here, $\delta \zeta_i$ are Gaussian processes which represent the perturbation to the ζ_i caused by the perturbation to the abundances. In particular, they satisfy $\langle \delta \zeta_i(t) \delta \zeta_j(s) \rangle_{x^*} = \delta_{ij} S^{-1} \sum_k \langle \delta x_k(t) \delta x_k(s) \rangle_{x^*}$. The averages are with respect to the stochastic process $\delta \zeta_i$, conditional on the x^* . Similarly, $\delta m_{\beta} = S_g^{-1} \sum_{i \in \beta} \langle \delta x_i(t) \rangle_{x^*}$ are perturbations to group abundances. The first term in Eq. (D1) is zero for surviving species, and it is negative for extinct species as per Eq. (C6). Thus, it always induces an exponential relaxation toward zero. We focus on the second term, which is nonzero for extant species only. Given that the $\delta \zeta_i$ are Gaussian and that the equation is linear, δx_i are Gaussian processes, which we can characterize through their first two moments. In particular, we will look for divergences in the averages $\langle \delta x_i(t) \rangle_{x^*}$ and in the power spectra $\langle |\delta \hat{x}_i(\omega)|^2 \rangle_{x^*}$.

1. FP/AF transition

We start by the power spectra which will signal the FP/AF transition. Assuming that the means do not diverge at the same time, we may follow [11,41] in supposing that $\delta m_\alpha = 0$. Then, taking the one-sided Fourier transform of Eq. (D1), and

squaring and averaging it, we obtain

$$\phi^{-1} \left(1 + \frac{\omega^2}{r_i^2 x_i^2} \right) \langle |\delta \hat{x}_i(\omega)|^2 \rangle_{x^*} = \langle |\delta \hat{\zeta}_i(\omega)|^2 \rangle_{x^*} + \left\langle \frac{\delta x_i(0)^2}{x_i^2} \right\rangle_{x^*}. \quad (\text{D2})$$

Further averaging with respect to species and focusing on the $\omega = 0$ mode (which is the first to diverge) yields

$$\langle |\delta \hat{x}(\omega)|^2 \rangle = \frac{\phi \langle \delta x_i(0)^2 / x_i^2 \rangle}{1 - \phi \sigma^2}, \quad (\text{D3})$$

where we have used $\langle |\delta \hat{\zeta}_i(\omega)|^2 \rangle_{x^*} = S^{-1} \sum_j \langle |\delta \hat{x}_j(\omega)|^2 \rangle_{x^*}$. The resonance in Eq. (D3) yields the instability condition, which is thus the same as the May transition of the rGLV

$$\phi \sigma^2 > 1. \quad (\text{D4})$$

For the RPS system, the fixed point has the same characteristics as that of the rGLV, and thus the transition is located at $\phi = 1/2$ and $\sigma = \sqrt{2}$. For other systems, Eq. (D4) still holds, but ϕ might depend on structure and thus the transition might not happen at $\sigma = \sqrt{2}$.

2. SO/FP transition

Our main result concerns divergences in the averages, where a deeper interplay between randomness and structure takes place. Using the fact that $\langle \delta \zeta_i \rangle_{x^*} = 0$, we can take the average of Eq. (D1) to obtain

$$\frac{d}{dt} \langle \delta x_i \rangle_{x^*} = r_i x_i^* \left(-\langle \delta x_i \rangle_{x^*} - \sum_{\beta} M_{\alpha\beta} \delta m_{\beta} \right). \quad (\text{D5})$$

Using the fact that $\delta m_{\beta}(t) = S_g^{-1} \sum_{j \in \beta} \langle \delta x_j(t) \rangle_{x^*}$, we can rewrite Eq. (D5) as

$$\frac{d}{dt} \langle \delta x_i \rangle_{x^*} = \sum_j B_{ij} \langle \delta x_j \rangle_{x^*} \quad (\text{D6})$$

with the $S \times S$ matrix $B_{ij} = -r_i x_i^* (\delta_{ij} + S_g^{-1} \mu_{ij})$. An instability in the mean is signaled by any eigenvalue of B having a vanishing real part. In the main text, we have defined the pseudo-Jacobian of RPS $\mathcal{J} = B/(1 - \tilde{\kappa}m)$, which has the same stability properties as B , since $1 - \tilde{\kappa}m > 0$.

3. Divergent transition

For completeness, we characterize here the divergent transition. For the RPS, this transition is the same as that of the rGLV studied in [10,11]. For the general model Eq. (2), we can use the characterization $q \rightarrow \infty$ in Eq. (C7) to obtain

$$g_{\alpha} = \omega_1 \left(-\sum_{\beta} M_{\alpha\beta} g_{\beta} \right) \\ 1 = \sigma^2 G^{-1} \sum_{\alpha} \omega_2 \left(-\sum_{\beta} M_{\alpha\beta} g_{\beta} \right), \quad (\text{D7})$$

where $g_{\alpha} = m_{\alpha}/\sigma\sqrt{q}$ remains finite at the transition. Given $M_{\alpha\beta}$, the first equations can be numerically solved to obtain g_{α} , which can then be plugged into the second line to obtain σ . For the RPS, these simplify to $g = \omega_1(-\tilde{\kappa}g)$ and $\sigma^2 = 1/\omega_2(-\tilde{\kappa}g)$.

APPENDIX E: EFFECT OF ABUNDANCE SPREAD ON EIGENVALUES

To study the spectrum of $\mathcal{J}$, we can take advantage of the low rank of $(\mu_{ij})_{i,j \leq S}$ to reduce the problem to that of inverting a small matrix. In particular, we may write $\mu_{ij} = \sum_{\alpha\beta} \epsilon_{i\alpha} M_{\alpha\beta} \epsilon_{j\beta}$, where $\epsilon_{i\alpha} = 1$ if i is in α and zero otherwise, and use Woodbury's matrix identity to obtain that the eigenvalues of $\mathcal{J}$ satisfy

$$\det \left(M^{-1} + \epsilon^T \text{diag} \left(\frac{z_i}{\lambda(\sigma) + z_i} \right) \epsilon \right) = 0, \quad (\text{E1})$$

where the matrix in the determinant is now $G \times G$. From Eq. (4), the abundances of species belonging to the same group follow the same probability distribution, so that we may rewrite this as

$$\det \left(M^{-1} + \text{diag} \left(\frac{z_{\alpha}}{\lambda(\sigma) + z_{\alpha}} \right) \right) = 0, \quad (\text{E2})$$

where the diagonal matrix is now $G \times G$, and z_{α} is the common distribution of z_i for i in group α . A generalization of Eq. (E2) to non-symmetric matrices is given in SM [42].

As discussed in the main text and Appendix C, any system for which $\vec{1}$ is an eigenvector of M (like the RPS) has a fixed point which is independent on the macroscopic structure. In particular, for this class of fixed points, all groups have the same abundance distribution, so that Eq. (E2) simplifies to the condition that $- \langle z / (\lambda(\sigma) + z) \rangle$ is an eigenvalue of M^{-1} . Introducing $\langle \dots \rangle_{z>0} = \phi^{-1} \langle \dots \rangle$ and using the fact that $M = -(\mathbb{I} + J^M)$ finally gives Eq. (7).

For real eigenvalues, the concavity of the function inside the brackets in Eq. (7) implies that $\lambda(\sigma)/\langle z \rangle_{z>0} \leq \phi(\sigma)(1 + \lambda_0) - 1$. In particular, decreasing ϕ decreases $\text{Re } \lambda(\sigma)$ and stabilization happens for $\phi \leq 1/(1 + \text{Re } \lambda_0)$. We can artificially set ϕ to 1 in order to remove the stabilizing effect of extinctions and focus on the stabilizing effect that abundance spread has on the average of Eq. (7).

The flow of Eq. (8) is then obtained by differentiating Eq. (7). We do so by defining a set of processes $\{y_i^{\sigma}\}_{\sigma \geq 0}$ such that $y_i^0 = 1$ and $y_i^{\sigma+d\sigma} = y_i^{\sigma} + \sqrt{\eta'(\sigma)} dW_i^{\sigma}$, where W_i are independent Brownian motions. Conditioned on positivity, y_i^{σ} has the same law as z_i for a disorder strength of σ . Plugging the evolution equation for y_i in Eq. (7) and developing to leading order in $\delta\lambda(\sigma)$ and δy_i^{σ} , we obtain

$$\delta\lambda = -\eta'(\sigma) \lambda \left\langle \frac{1}{(\lambda + y^{\sigma})^3} \right\rangle_{y^{\sigma}>0} \left\langle \frac{z}{(\lambda + y^{\sigma})^2} \right\rangle_{y^{\sigma}>0}^{-1} \delta\sigma. \quad (\text{E3})$$

Rearranging and writing the averages explicitly in terms of the distribution of y^{σ} gives Eq. (8).

- [1] J. Bergelson, M. Kreitman, D. A. Petrov, A. Sanchez, and M. Tikhonov, *eLife* **10**, e67646 (2021).
- [2] J. E. Goldford, N. Lu, D. Bajić, S. Estrela, M. Tikhonov, A. Sanchez-Gorostiaga, D. Segrè, P. Mehta, and A. Sanchez, *Science* **361**, 469 (2018).
- [3] S. Louca, M. F. Polz, F. Mazel, M. B. N. Albright, J. A. Huber, M. I. O'Connor, M. Ackermann, A. S. Hahn, D. S. Srivastava, S. A. Crowe, M. Doebeli, and L. W. Parfrey, *Nat. Ecol. Evol.* **2**, 936 (2018).
- [4] L. M. O. Laureto, M. V. Cianciaruso, and D. S. M. Samia, *Nat. & Cons.* **13**, 112 (2015).
- [5] F. S. Chapin, P. A. Matson, H. A. Mooney, and P. M. Vitousek, *Principles of Terrestrial Ecosystem Ecology* (Springer, New York, NY, 2002).
- [6] J. Moran and M. Tikhonov, *Phys. Rev. X* **12**, 021038 (2022).
- [7] F. Roy, G. Biroli, G. Bunin, and C. Cammarota, *J. Phys. A: Math. Theor.* **52**, 484001 (2019).
- [8] I. Akjouj, M. Barbier, M. Clenet, W. Hachem, M. Maïda, F. Massol, J. Najim, and V. C. Tran, *Proc. R. Soc. A* **480**, 20230284 (2024).
- [9] R. M. May, *Nature (London)* **238**, 413 (1972).
- [10] G. Bunin, *Phys. Rev. E* **95**, 042414 (2017).
- [11] T. Galla, *Europhys. Lett.* **123**, 48004 (2018).
- [12] J. I. Park, D.-S. Lee, S. H. Lee, and H. J. Park, *Phys. Rev. Lett.* **133**, 198402 (2024).
- [13] J. A. Vano, J. C. Wildenberg, M. B. Anderson, J. K. Noel, and J. C. Sprott, *Nonlinearity* **19**, 2391 (2006).
- [14] A. Arneodo, P. Coullet, and C. Tresser, *Phys. Lett. A* **79**, 259 (1980).
- [15] Z. Lu and Y. Luo, *Comput. Math. Appl.* **44**, 51 (2002).
- [16] S. Diederich and M. Oppen, *Phys. Rev. A* **39**, 4333 (1989).
- [17] T. A. de Pirey and G. Bunin, *Phys. Rev. X* **14**, 011037 (2024).
- [18] T. A. de Pirey and G. Bunin, *Phys. Rev. Lett.* **130**, 098401 (2023).
- [19] G. Bunin, [arXiv:1607.04734](https://arxiv.org/abs/1607.04734).
- [20] S. De Monte, F. d'Ovidio, and E. Mosekilde, *Phys. Rev. Lett.* **90**, 054102 (2003).
- [21] P. Kaluza and H. Meyer-Ortmanns, *Chaos* **20**, 043111 (2010).
- [22] G. Saxena, A. Prasad, and R. Ramaswamy, *Phys. Rep.* **521**, 205 (2012).
- [23] W. Zou, M. Zhan, and J. Kurths, *Phys. Rev. E* **98**, 062209 (2018).
- [24] S. D. Monte and F. d'Ovidio, *Europhys. Lett.* **58**, 21 (2002).
- [25] V. Ros, F. Roy, G. Biroli, G. Bunin, and A. M. Turner, *Phys. Rev. Lett.* **130**, 257401 (2023).
- [26] X. Gabaix, *Q. J. Econ.* **114**, 739 (1999).
- [27] L. Mills, M. Soulé, and D. Doak, *BioScience* **43**, 219 (1993).
- [28] J. Grilli, *Nat. Commun.* **11**, 4743 (2020).
- [29] A. Martin-Platero, B. Cleary, K. Kauffman, S. Preheim, D. McGillicuddy, E. Alm, and M. Polz, *Nat. Commun.* **9**, 266 (2018).
- [30] T. L. Rogers, S. B. Munch, S.-i. S. Matsuzaki, and C. C. Symons, *Ecol. Lett.* **26**, 470 (2023).
- [31] J. Hu, D. R. Amor, M. Barbier, G. Bunin, and J. Gore, *Science* **378**, 85 (2022).
- [32] S. Louca, S. M. S. Jacques, A. P. F. Pires, J. S. Leal, D. S. Srivastava, L. W. Parfrey, V. F. Farjalla, and M. Doebeli, *Nat. Ecol. Evol.* **1**, 0015 (2016).
- [33] G. Jack, J. Steele, J. Caporaso, L. Steinbrück, J. Reeder, B. Temperton, S. Huse, A. McHardy, R. Knight, I. Joint, P. Somerfield, J. Fuhrman, and F. Dawn, *The ISME Journal* **6**, 298 (2011).
- [34] C. Mutshinda, Z. Finkel, C. Widdicombe, and A. Irwin, *Funct. Ecol.* **30**, 1714 (2016).
- [35] D. Craven, N. Eisenhauer, W. Pearse, Y. Hautier, F. Isbell, C. Roscher, M. Bahn, C. Beierkuhnlein, G. Bönisch, N. Buchmann, C. Byun, J. Catford, B. Cerabolini, J. Cornelissen, J. Craine, E. De Luca, A. Ebeling, J. Griffin, A. Hector, and P. Manning, *Nat. Ecol. Evol.* **2**, 1579 (2018).
- [36] L. M. Thibaut and S. R. Connolly, *Ecol. Lett.* **16**, 140 (2012).
- [37] A. Gonzalez and M. Loreau, *Annu. Rev. Ecol. Evol. Syst.* **40**, 393 (2009).
- [38] B. L. Brown, A. L. Downing, and M. A. Leibold, *Ecology* **97**, 2021 (2016).
- [39] A. Goyal, L. S. Bittleston, G. E. Leventhal, L. Lu, and O. X. Cordero, *Elife* **11**, e74987 (2022).
- [40] A. Ba, I. Cvijović, J. Echenique, K. Lawrence, A. Rego-Costa, X. Liu, S. Levy, and M. Desai, *Nature (London)* **575**, 494 (2019).
- [41] J. Giral Martínez, M. Barbier, and S. De Monte, *bioRxiv*, (2024), doi: [10.1101/2024.11.25.624858](https://doi.org/10.1101/2024.11.25.624858).
- [42] See Supplemental Material at <http://link.aps.org/supplemental/10.1103/5w5x-b1c2> for further ecological context and a generalization to non-symmetric matrices.