


**Local and extensive fluctuations in sparsely interacting ecological communities**

Stav Marcus, Ari M. Turner, and Guy Bunin

*Department of Physics, Technion–Israel Institute of Technology, Haifa 32000, Israel* (Received 6 September 2023; revised 14 February 2024; accepted 30 May 2024; published 20 June 2024)

Ecological communities with many species can be classified into dynamical phases. In systems with all-to-all interactions, a phase where species abundances always reach a fixed point and a phase where they continuously fluctuate have been found. The dynamics when interactions are sparse, with each species interacting with only a few others, has remained largely unexplored. Here we study a system of sparse interactions, first when interactions are of constant strength and completely unidirectional, and then when adding variability and bidirectionality. We show that in this case a phase unique to the sparse setting appears in the phase diagram, where for the same control parameters different communities may reach either a fixed point or a state where the abundances of only a finite subset of species fluctuate, and we calculate the probability for each outcome. These fluctuating species are organized around short cycles in the interaction graph, and their abundances undergo large nonlinear fluctuations. We characterize the approach from this phase to a phase with extensively many fluctuating species, and show that the probability of fluctuations grows continuously to one as the transition is approached, and that the number of fluctuating species diverges. This is qualitatively distinct from the transition to extensive fluctuations coming from a fixed point phase, which is marked by a loss of linear stability. The differences are traced back to the emergent binary character of the dynamics when far from short cycles.

DOI: [10.1103/PhysRevE.109.064410](https://doi.org/10.1103/PhysRevE.109.064410)**I. INTRODUCTION**

Ecosystems can be extremely diverse [1], and the large numbers of species make statistical mechanics a powerful tool in addressing such systems. Theoretical and experimental work has revealed dynamical phases with distinct behavior [2–11], with a notable example being a transition from a phase where the dynamics from any initial conditions reach fixed points to one where variables fluctuate indefinitely, which is marked by a loss in the fixed points' stability [2–4,6,11]. Related transitions are also found in other fields [12–15].

Most research in the field has assumed that each species interacts with many others, where central-limit-type arguments apply [3,6,16]. Much less is known about sparsely interacting systems, where each species interacts significantly with only a handful of the (many) other species, despite evidence that such systems are ubiquitous in nature [17–20]. Previous works generalized relations between diversity and interaction properties [21] from fully interacting to sparse settings [22,23], and obtained statistics of the number of fixed points in the limit of strong interactions [24]. In [25] the species abundance distribution was analyzed at fixed points of sparsely interacting systems. For symmetric interactions, properties of fixed points [10] and activated dynamics [9] have been found to differ dramatically from their fully connected counterparts. This work will focus on long-time deterministic dynamics, irrelevant in systems with symmetric interactions, which always eventually reach fixed points [26,27].

Here we study the dynamics of many-species sparsely interacting communities when interactions are far from symmetric. We first study a minimal model where interactions are unidirectional and detrimental to the affected species (i.e., amensalistic) and of equal strength. We then extend

the analysis to bidirectional interactions with variability in strength.

Our analysis reveals three phases, in both the minimal model and the more general model: (1) a fixed point (FP) phase, where dynamics always reach a stable fixed point; (2) an extensive fluctuations (EF) phase, where the abundances of a finite fraction of the species fluctuate; and (3) a local fluctuations (LF) phase, where the abundances of a finite number (not growing with system size) of clustered species may fluctuate, while the rest are fixed. The fluctuating species are localized around short loops in the interaction graph. This phase arises in the sparse setting and cannot appear when there are all-to-all interactions. We calculate  $p_{\text{fluc}}$  in this phase, the probability of sampling a system whose dynamics do not reach a fixed point, an experimentally accessible quantity of great interest [11]. We find that  $0 < p_{\text{fluc}} < 1$  even for many-species systems, in contrast to fully connected settings where  $p_{\text{fluc}} = 0$  or 1 in the fixed point and fluctuating phases respectively [3,16].

This paper focuses on the local fluctuations phase and the phase transitions between it and other phases, which are qualitatively different from those in fully interacting systems.

**II. MODEL DEFINITIONS**

We employ standard Lotka-Volterra dynamics, with migration from a species pool. The migration models the effect of migration to an “island” from a “mainland” and captures important phenomena of dynamical fluctuations and diversity [5,6,10,11,16,28–30]; these effects also appear in explicit spatial models [31–34]. The dynamics of the abundance (i.e., population size)  $N_i$  of species  $i$  in the local community is

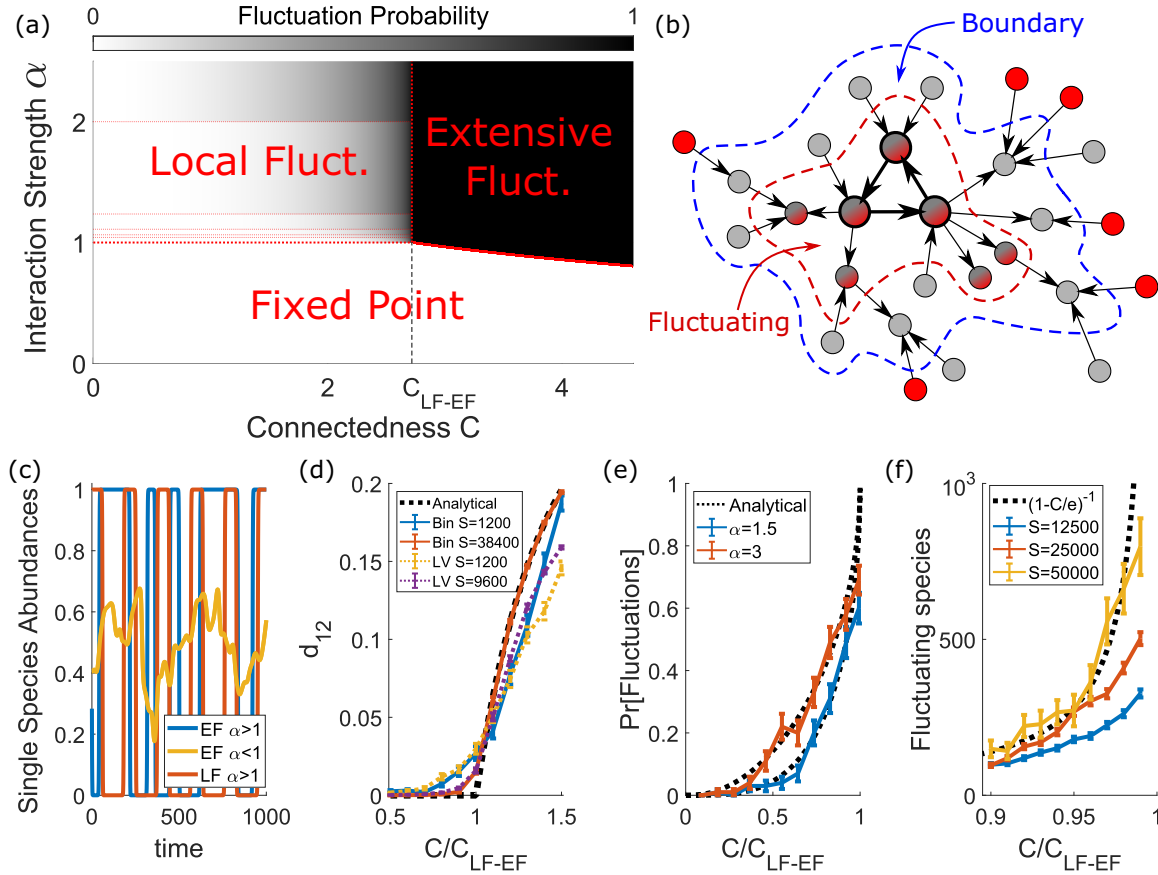


FIG. 1. The minimal model. (a) Phase diagram and fluctuation probability in the space of connectedness  $C$  and interaction strength  $\alpha$ . Thick red lines mark transition lines between phases, and thin lines in the local fluctuations (LF) phase mark discontinuous jumps in fluctuation probability, at the values  $\alpha_c(n)$ . (b) A short three-species cycle that fluctuates in the LF phase at  $\alpha > \alpha_c(3) = 2$  and its neighborhood. Shown are  $N_i = 1$  species (red),  $N_i = 0$  (gray), and fluctuating  $N_i$  (red-gray). (c) Examples of abundance dynamics of single species in the Lotka-Volterra model, in the LF phase, and in the extensive fluctuations (EF) phase for  $\alpha > 1$  and  $\alpha < 1$ . (d) The steady-state distance  $d_{12}$  between copies of the same system initiated with different initial condition as a function of  $C$ . Analytical results are compared with simulations of the Lotka-Volterra and binary models. (e) The fluctuation probability  $p_{fluc}(C)$  in the Lotka-Volterra model, compared with the analytical result, for  $\alpha = 1.5 < \alpha_c^{(3)}$ ,  $\alpha = 3 > \alpha_c^{(3)}$ . The probability reaches 1 at the transition to the EF phase. (f) The average number of fluctuating species as a function of  $C$ , from binary model simulations, and the expected behavior  $(1 - C/C_{LF-EF})^{-1}$  near the transition.

given by

$$\frac{dN_i}{dt} = N_i \left( K_i - \sum_{j=1}^S \alpha_{ij} N_j \right) + \lambda_i. \quad (1)$$

The interspecies interaction strengths are  $\alpha_{ij}$ .  $K_i/\alpha_{ii}$  are carrying capacities (abundance reached if a species were alone), and as is often done we take all  $K_i = 1$  and  $\alpha_{ii} = 1$  [35]. The pool migration rates  $\lambda_i$  are taken to be small,  $\lambda_i = \lambda \ll 1$ . We start with a simple but enlightening version of the model. Here interaction strengths  $\alpha_{ij}$  for  $i \neq j$  are drawn independently, with  $\alpha_{ij} = \alpha$  with probability  $C/S$ , and  $\alpha_{ij} = 0$  otherwise.  $C$  is a model parameter called the connectedness. This setting is relevant when there are few significant interactions per species, with other interactions weak enough to be neglected. This corresponds to a directed Erdős-Rényi graph, with an edge from  $j$  to  $i$  if  $\alpha_{ij} = \alpha$ . This graph is sparse, with a fixed average number  $C$  of incoming edges per species, even as  $S \rightarrow \infty$ . Some known facts regarding these graphs are the following: almost all edges  $i \rightarrow j$  do not have a reverse  $j \rightarrow i$ ; the local neighborhood of almost all vertices is a tree

(no cycles); there are only a few cycles of any finite length (their average number doesn't scale with  $S$ ); and finite-length cycles are isolated (the distance between them grows with  $S$ ) [36]. Unidirectional interactions are taken as a starting point for understanding asymmetric interactions and the time-dependent phenomena that can occur for them, unlike for symmetric interactions where dynamics always reach fixed points [26]. The phase diagram in terms of the two parameters,  $C$  and  $\alpha$ , is shown in Fig. 1(a).

### III. ONSET OF EXTENSIVE FLUCTUATIONS

When  $\alpha > 1$ , we see two distinct dynamical behaviors depending on  $C$ , with a transition at  $C_{LF-EF}$ , which we show below to be  $C_{LF-EF} = e$ . For  $C < C_{LF-EF}$ , all species (except possibly a finite number near short cycles in the graph; see below) are fixed at either  $N_i \approx 1$  or  $N_i \approx 0$  (both to order  $\lambda_i$ , henceforth we write  $N_i = 0, 1$ ). Species fixed at  $N_i = 0$  are referred to as locally extinct, since they are present in small numbers, supported only by the migration. At  $\alpha > 1$  and  $C > C_{LF-EF}$ , an extensive number of species fluctuate. At small

$\lambda$ , and reasonable values of the interaction strength  $\alpha = O(1)$ , the fluctuating species spend most of the time near 0,1 [see Fig. 1(c)] with rapid switches between them for  $\lambda \ll 1$  (the fraction of time spent switching scales as  $1/|\ln \lambda|$ —see Appendix A—so switches appear more gradual at intermediate migration rates). The switches when  $\alpha > 1$  are due to competitive exclusion [37], where once a species has  $N_i = 1$  it then drives others to extinction.

These rapid switches can be captured by a model with binary variables,  $N_i \in \{0, 1\}$ , which is helpful in deriving the location of the transition and other properties. In it, a randomly chosen species  $i$  switches to  $N_i = 0$  if at least one of its incoming arrows have  $N_j = 1$ , and to  $N_i = 1$  otherwise, reflecting the growth or decline of  $N_i$  with such inputs in the Lotka-Volterra model. The switches are done at some constant rate, so the only free parameter is the connectedness  $C$ . (The overall rate depends on  $\alpha$ , but this changes only the timescale of the system.)

The binary model can be understood (including the location of the phase transition) by solving for certain extensive properties. First, consider the fraction of  $N_i = 1$  species at long times,  $\phi = \text{Pr}[N_i = 1]$ . For a typical species  $i$ , the values  $N_j$  of its incoming species are independent, since almost all cycles are long and so the species  $j$  do not affect one another. Using the requirement that after a switch  $N_i = 1$  if and only if all incoming  $N_j = 0$ , one obtains  $\phi = \sum_K P_K (1 - \phi)^K = e^{-C\phi}$ , where  $P_K = e^{-C} C^K / K!$  is the probability for  $K$  incoming edges. This is solved by  $\phi = W(C)/C$ , with  $W$  the Lambert  $W$  function. This is the same value of  $\phi$  found for fixed points in the limit of infinitely strong interactions by other methods [24]. The transition to the EF phase, marked by the appearance of persistent fluctuations, can be located using the technique of [38–40] as reviewed in Appendix C. It involves solving for the distance  $d_{12}(t) = \frac{1}{S} \sum_{i=1}^S |N_i^1(t) - N_i^2(t)|$  between two copies of the same system with different initial conditions  $\{N_i^1\}, \{N_i^2\}$  by writing a closed differential equation for it, depending also on the known  $\phi$ . The distance at long times is zero in the LF phase and increases continuously when increasing  $C$  above the transition point  $C = e$  [see Fig. 1(d)]. This means that above  $C = e$  there is no stable fixed point that is reached dynamically.

We conclude that in the binary model at  $\alpha > 1$  there is a transition at  $C \equiv C_{\text{LF-EF}} = e$  into an EF phase; see Fig. 1(d). The above analysis for the binary model also applies to the Lotka-Volterra model: For a fixed point in the Lotka-Volterra model,  $N_i \approx 0$  or  $N_i \approx 1$  away from short cycles. Then, just as for the binary model, each present species must have only extinct neighbors, and each extinct species must have an incoming interaction from a present neighbor. The argument for calculating  $\phi$  is therefore valid for the Lotka-Volterra model. Also, if a fixed point is stable in the binary model, it is also stable in the Lotka-Volterra model. Thus, the transition value  $C_{\text{LF-EF}} = e$  is exact, while the dynamics at  $C > C_{\text{LF-EF}}$  are qualitatively similar; see Fig. 1(d).

#### IV. LOCAL FLUCTUATIONS

We now turn to analyze local fluctuations in the Lotka-Volterra framework. As follows from the discussion above, for  $C < C_{\text{LF-EF}}$  and  $\alpha > 1$  the variables  $N_i$  reach a fixed value,

except possibly a subextensive fraction. We now characterize the structure of the fluctuating subsets, show that they are finite, and calculate the probability that such fluctuations occur.

Consider a local set of fluctuating species and the subgraph of the interactions between them. First, we argue that all the static species they interact with are extinct, so that the set is effectively isolated from the rest of the community. To do that, look at the set’s boundaries, i.e., species that interact with the fluctuating species but do not themselves fluctuate; see Fig. 1(b). If a boundary species  $N_j$  is upstream from a fluctuating species  $i$ , it must be extinct ( $N_j = 0$ ), otherwise it would not allow  $N_i$  to fluctuate: if  $N_j = 1$  and  $\alpha_{ij} > 1$ ,  $N_i$  would be prevented from growing. If this boundary species is downstream from the fluctuating species it must also be extinct, otherwise it too would fluctuate. Second, as the dynamics on any finite tree are known to always reach a fixed point [27], the fluctuating subset must include a single short cycle in the interaction graph (and no more than one, as finite-length cycles are rare and distant from each other in sparse graphs); see the example in Fig. 1(b). The fluctuating subset will then include the cycle and possibly downstream species, since species upstream from the cycle are unaffected by it.

Since all incoming species to the cycle are extinct, the cycle behaves as if it is isolated. In isolation, it can fluctuate only if it is directed, i.e., all interactions are directed in the same sense along the cycle (otherwise the cycle can be broken up into chains which must reach a fixed point), and only if it is of odd length (otherwise there is a stable fixed point where species along the cycle alternate between  $N_i = 0$  and  $N_i = 1$ ). On these cycles, there exists a fixed point where the  $N_i$ ’s are not 0,1, but instead  $N_i = 1/(1 + \alpha)$  for all the cycle species. There are fluctuations if this fixed point is unstable, with stability lost for  $\alpha > \alpha_c(n) = 1/\cos(\pi/n)$  for cycles with  $n$  species where  $n$  is odd; see Appendix B. So the cycle would fluctuate if  $\alpha > \alpha_c(n)$ , and with it the local variables downstream from it; see example in Fig. 1(b). The  $n = 3$  cycle, for example, is the well-known “rock-paper-scissors” configuration [41–43]. Note that in addition to there being fluctuations near a cycle, there is also a departure from the binary dynamics. When  $\alpha < \alpha_c$ , the fixed point has abundances along the cycle that are neither 0 or 1, which leads to downstream species having abundances that are also not 0,1 and are set by Eq. (1). Also, for  $\alpha$  larger than but close to  $\alpha_c(n)$ , the abundances do not switch between 0 and 1, but fluctuate between intermediate values. This also propagates downstream.

##### A. Fluctuation probability

As described above, fluctuations require three conditions: an odd directed cycle exists in the graph, it is unstable (this depends on  $\alpha$ ), and incoming interactions from boundary species do not drive cycle species to extinction. The probability that these three conditions are satisfied can be calculated exactly. The third condition requires that all the species upstream of any species in the cycle have abundances of zero. For each species  $i$  on the cycle, the probability that none of the incoming species will have  $N_j = 1$ , and therefore prevent  $N_i$  from fluctuating, is the same as the probability for a typical species (i.e., away from a cycle) not to be driven to extinction, which is exactly  $\phi$ . Thus, given a directed cycle of length  $n$

that fluctuates in isolation, the probability of fluctuating in the full graph is  $\phi^n$  (as different species have independent incoming links, as happens in a typical tree-like environment; see above). The number of directed cycles of length  $n$  is Poisson distributed with mean  $C^n/n$  [36]. Each fluctuates with probability  $\phi^n$ , so the number of fluctuating cycles of length  $n$  is Poisson distributed with mean  $m_n = (C\phi)^n/n = [W(C)]^n/n$  [using  $\phi = W(C)/C$ ]. The numbers of cycles of different lengths are independent, so the total number of fluctuating cycles of any length is Poisson distributed, say, with mean  $m$ . The probability of at least one cycle fluctuating is then  $p_{\text{fluc}} = 1 - e^{-m}$ . In the range  $\alpha_c(2n+1) < \alpha < \alpha_c(2n-1)$ ,

$$\begin{aligned} m &\equiv \sum_{j=n}^{\infty} \frac{[W(C)]^{2j+1}}{2j+1} \\ &= \frac{1}{2} \ln \left[ \frac{1+W(C)}{1-W(C)} \right] - \sum_{j=0}^{n-1} \frac{[W(C)]^{2j+1}}{2j+1}. \end{aligned} \quad (2)$$

The calculated probabilities are shown in Figs. 1(a) and 1(e); note that the probability jumps at the  $\alpha_c(n)$  where different cycles lose stability, and that the probability reaches 1 at  $C = C_{\text{LF-EF}}$  [since  $W(e) = 1$ ] for all  $\alpha > 1$ . As  $\alpha_c(n) \xrightarrow{n \rightarrow \infty} 1^+$ , when decreasing to  $\alpha < 1$  from the LF phase all cycles become stable, and the system enters the FP phase at  $\alpha_{\text{FP-LF}} = 1$ .

For the binary model, the probability of fluctuations can be found by noting that all odd cycles are unstable (if all upstream species are extinct). Therefore the probability is the same as in the Lotka-Volterra model when all cycles are unstable, i.e. for  $\alpha > \alpha_c(3)$ ,  $p_{\text{fluc}} = 1 - \frac{C}{W(C)} \sqrt{\frac{1-W(C)}{1+W(C)}}$ .

### B. Downstream effect of fluctuations

Now consider the total number of fluctuating species, including the species in fluctuating cycles as well as the ones downstream from them. A species on a fluctuating cycle may drive downstream species to fluctuate as well, and the fluctuations spread in this way until they are “blocked,” when a fluctuating species only links downstream to extinct species (if any). This downstream spread can be considered as a branching process, generating a downstream tree. The number of species driven to fluctuate by any fluctuating species is Poisson distributed. Denote the mean of this distribution by  $\rho(C)$ . As a species downstream from a fluctuating species is driven to fluctuate iff it is not driven extinct by other neighbors with  $N_j = 1$ , this occurs with probability  $\phi = \Pr[N_i = 1]$ ; and as the average number of outgoing edges is  $C$ , this gives  $\rho(C) = \phi C = W(C)$ . The downstream species from each species on the cycle (excluding its neighbor along the cycle) form a tree of fluctuating species. Such a tree can be shown to have a diverging average size when  $\rho(C) = 1$  [44], which occurs at  $C = C_{\text{LF-EF}} = e$ . The number of fluctuating species near the divergence grows as  $(1 - C/C_{\text{LF-EF}})^{-1}$ , a known result from branching processes [44]. This is shown in Fig. 1(f). This occurs at the same point as the transition to the EF phase, so there is no intermediate phase between the LF and EF phases. Above  $C_{\text{LF-EF}}$  the dynamics of small subgraphs can no longer be understood in isolation. As we use here only the extensive

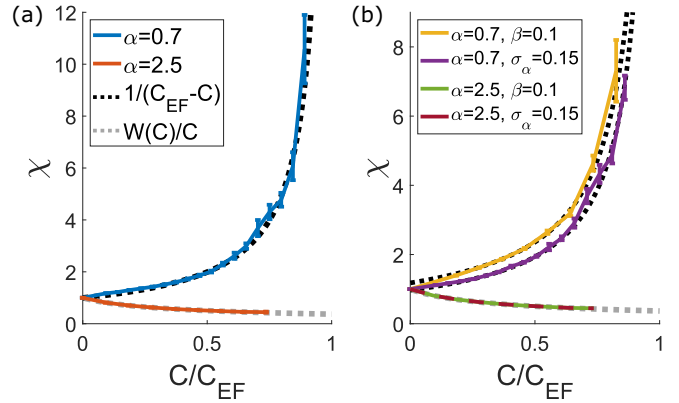


FIG. 2. The response  $\chi$  when approaching the EF phase by increasing the connectedness  $C$ . The x axis shows  $C/C_{\text{EF}}$  where “ $C_{\text{EF}}$ ” means  $C_{\text{LF-EF}}$  or  $C_{\text{FP-EF}}(\alpha)$ , depending on the transition. (a)  $\chi$  diverges when increasing  $C$  at constant  $\alpha$  coming from the FP phase, indicating a loss of stability. In contrast,  $\chi$  does not diverge when coming from the LF phase. The dotted black line is a fit to  $A(C_{\text{FP-EF}} - C)^{-1}$ , and the dotted gray line is the analytical result for  $\chi$  when coming from the LF phase. (b) The transition properties do not change when adding variability [ $\alpha_{ij} \neq 0$  are drawn from  $\text{Normal}(\alpha, \sigma_\alpha)$ ] and bidirectionality (for every  $\alpha_{ij} \neq 0$  the reverse interaction is  $\alpha_{ji} = \beta$ ) to the interactions. For  $\alpha = 0.7$ ,  $\chi$  still diverges as  $(C_{\text{FP-EF}} - C)^{-1}$ , and for  $\alpha = 2.5$ ,  $\chi = W(C)/C$  still holds.

value  $\phi$ , which is the same in the binary and Lotka-Volterra models, these results hold for both models.

A similar divergence in the number of fluctuating variables occurs in the “frozen phase” of binary models such as the Kauffman model [45]. In this context, the fluctuation probability  $p_{\text{fluc}}$  has not been calculated and may be of interest. Note, however, that the frozen phase has been discussed in the context of binary models, while for the Lotka-Volterra model fluctuations on the cycle may be between some intermediate values [for  $\alpha$  close to  $\alpha_c(n)$ ], as will be the fluctuations downstream from it.

### V. COMPARISON OF TRANSITIONS TO THE EF PHASE FROM THE FP AND LF PHASES

For  $\alpha < 1$ , at small values of  $C$ , the system is in the FP phase rather than the LF phase, in which the system always reaches a fixed point. Besides the possibility of local fluctuations in the LF phase, there are other distinctions between the FP and LF phases. Consider the response  $\chi$  to small changes in the carrying capacities  $K_i \rightarrow 1 + \varepsilon_i$ , with  $\varepsilon_i$  independent random numbers. Denoting by  $n_i$  the corresponding change in the fixed point value of  $N_i$ ,  $\chi$  is defined as  $(\sum_i n_i^2)/(\sum_i \varepsilon_i^2)$ . In systems with all-to-all interactions,  $\chi$  diverges when approaching the transition to a chaotic phase. This is tied to the closing of the gap in the spectrum of the matrix  $\{\alpha_{ij}\}$ , which is known to occur at this transition [3,6,16]. For the persistent species at a fixed point,  $\partial N_i/\partial K_j = (\alpha^{-1})_{ij}$ , and so  $\chi$  diverges when  $\alpha_{ij}$  has a zero eigenvalue. We find that  $\chi$  diverges also in sparse communities when approaching  $C_{\text{FP-EF}}(\alpha)$  from the FP phase; see Fig. 2.

This is very different from what happens in the transition from the LF phase: here  $\chi$  will turn out not to diverge at the

transition. First, the definition of  $\chi$  must be generalized to allow for fluctuations, by measuring the change in the time average of  $N_i(t)$  in response to the changes in  $K_i$ . In the LF phase, all but finitely many species are static with  $N_i = 0$  or 1, so these determine the value of  $\chi$  when  $S \rightarrow \infty$ . The species that do not fluctuate and have  $N_i = 1$  are isolated (surrounded by extinct species, if any), so one can see that  $n_i = \varepsilon_i$  for them, while for the species with  $N_i = 0$ ,  $n_i = 0$ . We therefore have  $\chi = \phi$ . Thus the response remains finite when approaching the transition from the LF phase. This could be expected as species are cut off from one another in the LF phase, which is what allows a small subgraph to fluctuate without leading to dynamics in the whole system.

## VI. BEYOND THE MINIMAL MODEL

The minimal model discussed so far assumes unidirectional interactions of constant strength  $\alpha$ . We conclude by discussing the robustness of the results when introducing changes to interaction coefficients. The distinction between the phases is robust when introducing variability in  $\alpha_{ij}$ , and bidirectionality (competitive rather than amensalistic interactions), namely,  $\alpha_{ji} \neq 0$  with a finite probability when  $\alpha_{ij} \neq 0$ . The results for the minimal model can be summarized as follows: In the LF phase, a hybrid binary-continuous behavior emerges, with most variables taking two values, while close to short cycles the variables might take values at  $N_i \notin \{0, 1\}$  and might fluctuate. The probability of fluctuations has  $0 < p_{\text{fluc}} < 1$ , and it reaches 1 at the transition to the EF phase, where the number of fluctuating species diverges and becomes extensive. Approaching the FP phase from the LF phase by lowering  $\alpha$ , cycles of ever-longer length become stable. This reduces the probability of fluctuations due to finite-length cycles, until  $p_{\text{fluc}} = 0$  when  $\alpha = 1$ .

In the LF phase in the minimal model, both the fluctuating subsets and species with fixed  $N_i = 1$  are isolated. Those properties are maintained when adding some variability and bidirectionality: The fluctuating subsets remain of finite size, because their downstream extension is limited by the chance of reaching an extinct species (that cannot fluctuate), and this probability depends continuously on the  $\alpha_{ij}$  values; while they remain isolated from species upstream from them, in spite of some bidirectionality, because these species are extinct. We prove in Appendix D, that assuming that all strong interactions are  $\alpha_{ij} > 1$  and the reverse  $\alpha_{ji} \geq 0$ , any species with  $N_i > 0$  that is far from cycles is isolated, just as in the minimal model. The terms ‘‘upstream’’ and ‘‘downstream’’ in this context would refer to the direction of the stronger interaction that is larger than 1 (if both  $\alpha_{ij}, \alpha_{ji} > 1$  the system always reaches a fixed point and is not in the LF phase [10]). Thus  $\chi = \phi$ , which is finite when approaching the transition; see Fig. 2(b). Simulations also confirm that in the LF phase, the number of fluctuating species is finite (as the distance  $d_{12}$  approaches zero for large  $S$ ) and that  $0 < p_{\text{fluc}} < 1$ , and that in the EF phase a finite fraction of species fluctuate (as  $d_{12}$  is finite for large  $S$ ) while  $p_{\text{fluc}} = 1$ ; see Fig. 3. Note that changes of  $\alpha_{ij}$  beyond some size may drive the system to other phases not discussed here, such as those found for symmetric interactions, where there can be no persistent fluctuations [9,10].

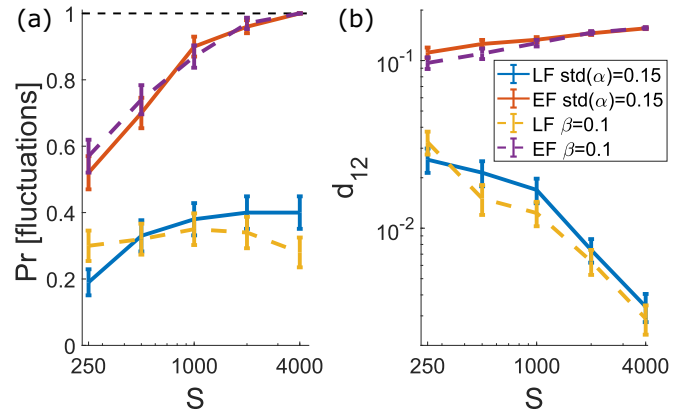


FIG. 3. Distinctions between the LF and EF phases are robust to adding bidirectionality and variability. Bidirectionality is added using  $\beta = 0.1$ , and variability by taking  $\text{std}(\alpha) = 0.15$ . We use the labels LF and EF to represent specific parameter sets used in these graphs and belonging in the two phases, which are  $(C, \alpha) = (2.5, 2.2), (2.5, 4)$  respectively. (a) The probability  $p_{\text{fluc}}$  as a function of system size  $S$ . (b) The long-time distance between copies of the same system initialized with different initial conditions, as a function of system size  $S$ .

In contrast, at low values of  $\alpha$  (the FP phase), increasing the connectedness  $C$  towards the EF phase is still accompanied by a divergence in  $\chi$ , even with the changes to the model; see Fig. 2(b). This is because the changes in  $\alpha_{ij}$  change the spectrum of the matrix  $\{\alpha_{ij}\}$  continuously, so the spectral gap still closes.

Consider now the distinction between the FP and LF phases themselves. Variability in  $\alpha_{ij}$  affects the stability of local cycles, so the sharp change in probability of local fluctuations at the boundary between the FP phase and LF phase is broadened. There remains, however, a sharp distinction between these phases in the decay of fluctuations away from a local perturbation: In the LF phase it is cut off at a finite distance (see above), while in the FP phase, the size of the fluctuations decays exponentially with the distance from the source of the fluctuations but extends arbitrarily far.

## VII. CONCLUSIONS AND DISCUSSION

We study the behavior of sparse ecological communities using the Lotka-Volterra framework. We start our analysis using a minimal model, where interactions are unidirectional and of constant strength. We find that in addition to a fixed point and extensive fluctuations phase, the system exhibits a local fluctuations phase at low connectedness and strong interactions, unique to the sparse setting. This phase cannot exist in fully interacting systems, which do not have the concept of locality in the interaction graph. The fluctuating species form local finite subgraphs, driven by short, odd-length directed cycles. The probability  $p_{\text{fluc}}$ , of sampling a system whose dynamics do not reach a fixed point, satisfies  $0 < p_{\text{fluc}} < 1$  even for many-species systems, in contrast to fully connected settings. The response  $\chi$  to changes in carrying capacities, which diverges at the transition to a fluctuating phase in fully connected system, remains finite in the transition between the local- and extensive-fluctuations phases. The existence of all

three phases is robust to the addition of variability and bidirectionality in interaction strengths, up to some finite strengths beyond which the system switches to other phases. Sharp distinctions remain in the behavior of  $\chi$  at the transitions to extensive fluctuations, and in the decay of fluctuations in the FP and LF phases: fluctuations are cut off at a finite distance from the cycles in the LF phase, but decay exponentially with the distance in the FP phase.

Our results suggest a perspective on why and when few-species models may be relevant in natural settings. Fluctuations in nature are often studied using models of only a few species [46–51], and the success of this approach would seem surprising as these few species are typically in interaction with other species in a diverse ecosystems [52]. In our model, we find that in the LF phase only a small number of species fluctuate appreciably: In the minimal model, their dynamics can be modeled as if in isolation, while when the interactions are bidirectional and variable, the dynamics may not be the same as if in isolation, but fluctuations are still concentrated on a few species. This gives a picture for why and when few-species descriptions work. In contrast, dynamical descriptions that only include a few species are expected to be problematic in the EF phase, where the dynamics of any finite subset of fluctuating species is inseparable from that of the entire system.

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#### APPENDIX A: MIGRATION SIZE EFFECTS

As mentioned in the main text, in the  $\alpha > 1$  range, the switches between the states  $N_i \approx 0, 1$  are more rapid for lower migration rates, with the ratio between the switch time and the sojourn time (the time spent in a given state between switching events) scaling as  $1/|\ln \lambda|$ . To understand this, consider first the abundance of an extinct species, growing from  $N_i \approx 0$  to  $N_i \approx 1$ . Prior to this, species  $i$  was extinct, meaning there was some incoming species  $j$  with  $\alpha_{ij} = \alpha$  and  $N_j = 1$ . At some time  $t_0$  species  $j$  switched to  $N_j \approx 0$ , allowing the abundance of  $N_i$  to grow. For some period of time before, for  $t < t_0$ , species  $i$  had a near-constant abundance,  $dN_i/dt \approx 0$ , giving  $N_i(t_0) = \lambda/(\alpha N_j - 1) = O(\lambda)$ . For  $t > t_0$ , one has  $dN_i/dt \approx N_i(1 - N_i) + \lambda \approx N_i$ . This is because all incoming species have  $N_j \approx 0$ , and because throughout most of the dynamics,  $\lambda \ll N_i \ll 1$ . The timescale for  $N_i$  to grow exponentially from  $O(\lambda)$  to  $O(1)$  is then  $\sim |\ln \lambda|$ . A similar timescale is derived and explained systematically in the chaotic dynamics phase in systems with all-to-all interactions [53].

On the other hand, as we take very small  $\lambda$ , below some threshold  $N^{\text{extinct}} \gg \lambda$  a species can be considered extinct. Say that we consider  $N_i \approx 0$  if  $N_i < N^{\text{extinct}} = 0.01$ . The time of the switch would be the time needed to grow from  $N^{\text{extinct}}$  to  $O(1)$ , which is independent of  $\lambda$ ; similarly, when a species goes from  $N_i \approx 1$  to  $N_i = N^{\text{extinct}}$ , the time of the switch would be independent of  $\lambda$ . Therefore, the timescale for the sojourn time at each state is  $\sim |\ln \lambda|$ , while the switches are independent of it. Consider Figs. 4(a)–4(d), showing the dynamics of a single species for  $\lambda = 10^{-3}, 10^{-10}$ , in both the LF and EF phases. For the larger value of  $\lambda$ , the timescale of the switches

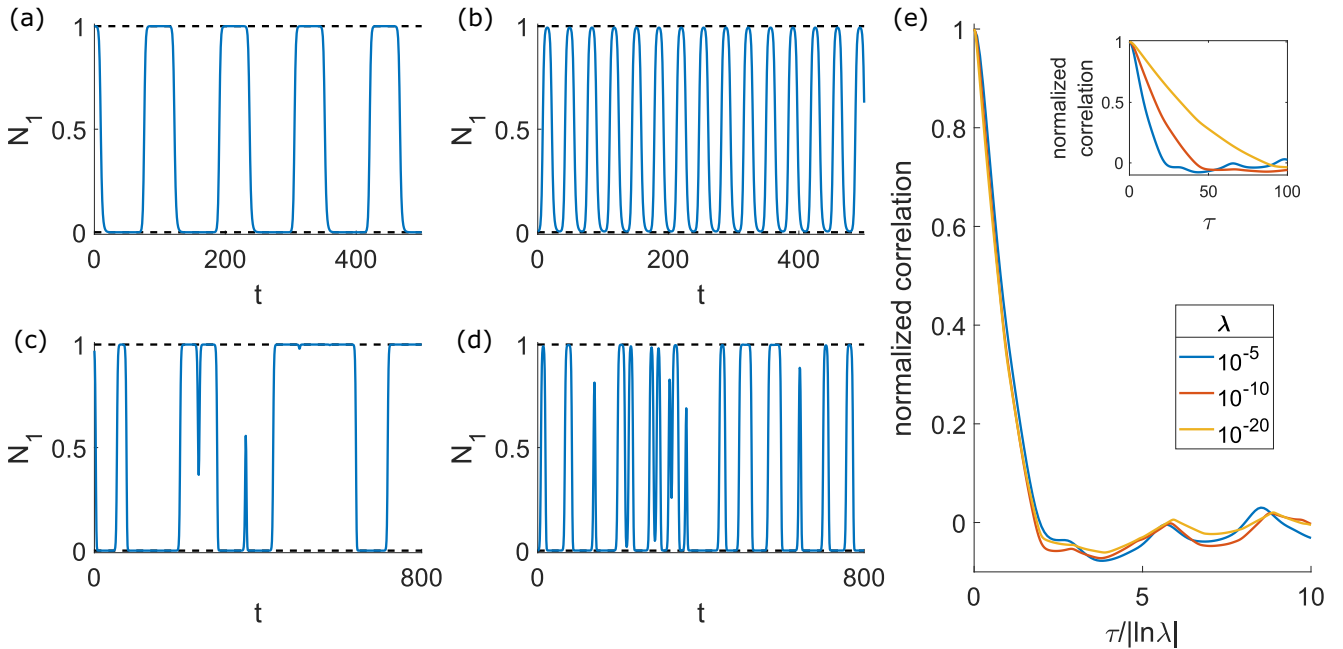


FIG. 4. The sojourn times depend on the migration rate. (a)–(d) The dynamics of a single species  $N_i(t)$  which is part of a system with  $S = 1000$ ,  $\alpha = 2.5$ . In the left column, the migration rate of all species is  $\lambda = 10^{-10}$ , and on the right it is  $\lambda = 10^{-3}$ . In (a)–(b) the system is in the LF phase, with  $C = 2$ . The species is part of a cycle generating the local dynamics. In (c)–(d) the system is in the EF phase, with  $C = 4$ . (e) The correlation  $C(\tau)$  for three different migration rates, averaged over systems in the EF phase, with  $S = 1000$ ,  $C = 3.5$ , and  $\alpha = 3$ . For each value of the migration, the correlation is normalized so that at  $C(\tau = 0) = 1$ ,  $C(\tau \rightarrow \infty) = 0$ . The correlations for the different migrations collapse to the same curve when rescaling  $\tau$  by  $|\ln \lambda|$ . Inset: the same curves when  $\tau$  is not rescaled.

is closer to that of the sojourn times. In the EF phase, this also results in “spikes” in  $N_i(t)$ : this happens when the species incoming to  $N_i$  start to change their states before the switch time is complete. This effect decreases as  $\lambda$  decreases and the sojourn times become longer.

The dependence on the migration rate  $\lambda$  can also be observed by studying the time autocorrelation  $C(\tau) = \langle \sum_i N_i(t)N_i(t+\tau)/S \rangle_t$ , which scales with  $\tau$  as  $|\ln \lambda|$ ; see Fig. 4(e).

We can also consider the dependence of switch rates on  $\alpha$ . The rate of a switch from  $N_i = N^{\text{extinct}}$  to  $N_i \approx 1$  will be independent of  $\alpha$ , and from the expression for  $N_i(t_0)$ , the decrease in sojourn time as  $\alpha$  is increased will scale as  $|\ln(\alpha - 1)|$ . As realistic values of  $\alpha$  are  $O(1)$ , in this range there will not be a very significant change in the sojourn times. Specifically, for the weak migration rates that we use, the rate of the switch will be much faster than the sojourn times.

### APPENDIX B: FLUCTUATIONS IN SHORT CYCLES

Here we prove that for isolated, directed cycles of odd length  $n$ , fluctuations occur for  $\alpha > \alpha_c(n) = 1/\cos(\pi/n)$ , by showing that they have no stable fixed point in this range. For a cycle of length  $n$ , we label the species as  $N_1, \dots, N_n$ , with species  $i - 1$  affecting species  $i$ . There are two possible kinds of fixed points, as either at least one species has  $N_i = 0$ , or all species have the same nonzero abundance  $N_i = 1/(1 + \alpha)$ . If all  $N_i > 0$ , the fixed point is stable if the  $\alpha_{ij}$  matrix is stable. Using the eigenvalues for an  $n \times n$  circulant matrix [54], one finds that this fixed point is stable for odd  $n$  for  $\alpha < 1/\cos(\pi/n)$ . We will now show that there can be no

stable fixed point in which there are extinct species, so for  $\alpha > \alpha_{\text{cycle}}$  there will be fluctuations.

Assume by contradiction that the cycle has a stable fixed point with extinct species. As  $n$  is odd, it must have at least two consecutive species that both have either  $N_i = 0$  or  $N_i > 0$ . If there is a set of consecutive species with  $N_i > 0$ , denote as  $j$  the first species in this chain, so that  $N_j = 1$ . Therefore  $N_{j+1} = 1 - \alpha N_j = 1 - \alpha < 0$ , in contradiction to the assumption. If there are consecutive species with  $N_i = 0$ , again denote  $j$  as the first in the chain. Then species  $j + 1$  has a positive growth rate,  $g_{j+1} = 1 - \alpha N_j = 1$ , so the fixed point is not stable to small positive perturbations in  $N_{j+1}$ , again in contradiction to the assumption.

### APPENDIX C: DISTANCES IN THE BINARY MODEL

In a binary model, at each time step  $dt = 1/S$  a random species is chosen to be updated according to

$$N_i(t + dt) = \begin{cases} 1 & \text{if all incoming arrows } j \rightarrow i \text{ have } N_j = 0 \\ 0 & \text{otherwise} \end{cases}, \quad (\text{C1})$$

where for two copies of the same system,  $\{N_i^1\}, \{N_i^2\}$ , the same species is updated at each step. Defining the per-species distance  $d_{12,i} = \Pr[N_i^1 \neq N_i^2]$  (with the probability over the choice of initial conditions and system disorder), the total distance is  $d_{12} = S^{-1} \sum_i d_{12,i}$ . Say that species  $N_i$  which has  $K$  incoming interactions from  $N_{j_1}, \dots, N_{j_K}$  is updated at time  $t$ . Then as  $N_{j_1}, \dots, N_{j_K}$  are independent (as almost all cycles are long), and noting that  $\Pr[(N_i^1, N_i^2) = (0, 0)] = 1 - \phi - d_{12,i}/2$ ,

$$\begin{aligned} d_{12,i}(t + dt) &= 2 \Pr [N_i^1(t + dt) = 1, N_i^2(t + dt) = 0] = 2 \left\{ \prod_{r=1}^K \Pr [N_{j_r}^1(t) = 0] - \prod_{r=1}^K \Pr [(N_{j_r}^1(t), N_{j_r}^2(t)) = (0, 0)] \right\} \\ &= 2[(1 - \phi)^K - (1 - \phi - d_{12}(t)/2)^K], \end{aligned}$$

averaging over the choice of interactions, initial conditions, and updated species the total distance obeys

$$\begin{aligned} d_{12}(t + dt) &= \frac{2}{S} \sum_K P_K [(1 - \phi)^K - (1 - \phi - d_{12}(t)/2)^K] \\ &\quad + (1 - 1/S)d_{12}(t) \end{aligned}$$

and using  $dt = 1/S$ ,  $P_K = e^{-C} \frac{C^K}{K!}$

$$\begin{aligned} \frac{d}{dt} d_{12} &= 2 \sum_K e^{-C} \frac{C^K}{K!} [(1 - \phi)^K - (1 - \phi - d_{12}/2)^K] - d_{12} \\ &= 2e^{-C} \phi \left[ 1 - e^{-\frac{1}{2} C d_{12}} \right] - d_{12}. \end{aligned}$$

This has a fixed point at  $d_{12} = 0$  for any  $C$ . Using  $\phi = W(C)/C$ , this fixed point loses stability at  $C = e$ , where a new stable fixed point appears growing continuously from 0:

$$d_{12}^* = 2[W(C) + W(-W^2(C)/C)]/C; \quad (\text{C2})$$

$d_{12}^*$  has a maximum at  $C \approx 7.14$ . For  $C \gg 1$ ,  $d_{12}^* \approx 2\phi$ , implying that there is no extensive overlap between the sets of species that have  $N_i = 1$  in the two copies.  $\phi$  disappears as  $C \rightarrow \infty$ , so at this limit also  $d_{12}^* \rightarrow 0$ .

### APPENDIX D: SPECIES WITH $N_i = 1$ ARE ISOLATED IN THE LF PHASE WHEN AWAY FROM SHORT CYCLES, WHEN ADDING VARIABILITY AND BIDIRECTIONALITY

In the main text we show that for the minimal model (unidirectional constant-strength interactions), for  $\alpha > 1$  and far away from short cycles, the abundances are fixed at either  $N_i = 0, 1$ , with the  $N_i = 1$  species separated from each other by extinct species. Here we will prove that this also holds when there are positive bidirectional interactions as well as bounded variability in the interaction strengths.

Consider a system where for any interaction with  $\alpha_{ij} = \alpha > 1$ , the reciprocal interaction is  $\alpha_{ji} = \beta > 0$ . Adding variability to these values will not change the proof, as long as

the probability distribution is bounded so that  $\alpha_{ij} > 1$  and  $\alpha_{ji} > 0$ . We assume that there are no extensive subgraphs of adjacent persistent species, so we focus on finite subgraphs. As the Erdős-Rényi graph is tree-like almost everywhere, and we are interested in the behavior far from the short cycles, we need only show that there are no finite tree-like subgraphs whose sites can all have  $N_i > 0$  at a fixed point, except for a single species in isolation.

Let us consider the Lotka-Volterra equations on a finite connected tree with at least two species, and assume for the sake of a contradiction that it has a stable fixed point where all species coexist with values  $N_i^* > 0$ . The variables  $N_i$  can be rescaled so that the interactions are symmetrized in the following manner [27]. Take new variables  $n_i = N_i/\gamma_i$ , with  $\gamma_i$  some constants to be chosen later. The equation then gives a new Lotka-Volterra system

$$\begin{aligned} \frac{dn_i}{dt} &= \gamma_i n_i (1/\gamma_i - n_i - \sum_j (\gamma_j/\gamma_i) \alpha_{ij} n_j) \\ &\equiv \gamma_i n_i \left( 1/\gamma_i - n_i - \sum_j a_{ij} n_j \right), \end{aligned} \quad (\text{D1})$$

with interaction matrix  $a_{ij} = (\gamma_j/\gamma_i) \alpha_{ij}$ . The  $\gamma_i$ 's are chosen as follows: choose some species  $i$  on the tree which interacts with species  $j_n$ ,  $n = 1, \dots, K$ , and take  $\gamma_i = 1$ . For each  $j_n$ , in order to have a symmetric interaction  $a_{ij_n} = a_{j_n i}$  one must set  $\gamma_{j_n} = \gamma_i \sqrt{\alpha_{j_n i}/\alpha_{ij_n}}$ . As all  $\alpha_{ij_n}, \alpha_{j_n i} > 0$ , this choice of  $\gamma_{j_n}$  is real and positive. This procedure is iterated for the species that interact with the  $j_n$  species, and so on until the values of  $\gamma_i$  are set for the entire tree. As the tree has no loops this procedure does not lead into any loops where variables are redefined.

Now consider the fixed point of (D1),  $n_i^* = N_i^*/\gamma_i$ . As  $\gamma_i > 0$ , this is a feasible fixed point with all  $n_i^* > 0$ , and from the assumption it is also stable. This must be the only stable fixed point of the system, as a symmetric Lotka-Volterra system has a stable fixed point where all species coexist iff it has a unique fixed point [10].

We will now show in contradiction that another stable fixed point can be constructed. Consider a new  $\tilde{N}_i$  system, which is the same as the original  $N_i$  system but with  $\beta = 0$ . Consider all species that have no incoming interactions (there must be

at least one on a tree), which must have  $\tilde{N}_i = 1$  at a fixed point. All outgoing interactions from these species must have  $\tilde{N}_i = 0$ , and continuing to move downstream all  $\tilde{N}_i$  will be uniquely determined to have either  $\tilde{N}_i = 0$  or  $\tilde{N}_i = 1$ . The fixed point found in this way is also a stable fixed point of the  $N_i$  system. This gives a fixed point with some  $n_i = 1/\gamma_i$  and some  $n_i = 0$ , which is different from  $n_i^*$ , where for all  $i$ ,  $n_i^* > 0$ , in contradiction to the assumption.

## APPENDIX E: DETAILS OF SIMULATIONS

Here we add details on the simulations and their results shown in the figures in the main text.

For each value of the connectedness  $C$ , couplings  $\alpha_{ij}$  are chosen independently, with each  $\alpha_{ij}$  taken to be nonzero with probability  $C/S$ . For Fig. 2, where there is a variance in the interaction strengths, we first choose the  $\alpha_{ij}$  that are nonzero, then sample the value from a normal distribution with mean  $\alpha$  and variance  $\sigma_\alpha^2$ . The Lotka-Volterra equations are solved with an ODE45 solver using  $K_i = 1$ ,  $\lambda_i = 10^{-10}$  (unless stated otherwise) and initial conditions are drawn from a uniform distribution on  $[0, 1]$ .

When modeling the binary system, we use initial conditions where each species has an equal probability to be either  $N_i = 0$  or  $N_i = 1$ . At each step, we choose a species randomly and update it using Eq. (C1). When calculating  $d_{12}$ , we take two systems with the same  $\alpha_{ij}$  and initiate each at two random initial conditions, then advance them simultaneously, choosing the same species to update at each step.

In Fig. 1(c) the example for the EF phase for  $\alpha > 1$  is taken from a system with  $S = 1000$ ,  $C = 4$ ,  $\alpha = 3$ , and for  $\alpha < 1$  from a system with  $S = 3000$ ,  $C = 5$ ,  $\alpha = 0.9$ . The example in the LF phase is from a system with  $S = 1000$ ,  $C = 1.5$ ,  $\alpha = 3$ . In Fig. 1(d) the results for Lotka-Volterra simulations are for  $\alpha = 3$ . In Fig. 1(e) the probabilities are taken for systems of size  $S = 1000$ .

In Fig. 2(a)  $C_{\text{LF-EF}} = e$  for  $\alpha = 2.5$  (as proven in the text). When coming from the FP phase with  $\alpha = 0.7$ , we find  $C_{\text{FP-EF}} \approx 5.3$  from a fit to points at  $C > 2$ . In Fig. 2(b), for both  $\alpha = 0.7$  and  $\alpha = 2.5$ , we introduce bidirectionality by setting  $\alpha_{ji} = \beta = 0.1$  when  $\alpha_{ij} = \alpha$ , or add variability by drawing the nonzero  $\alpha_{ij}$  from a normal distribution  $\mathcal{N}(\alpha, 0.15)$ . For  $\alpha = 0.7$ , the transitions occur at  $C_{\text{FP-EF}} \approx 4.9, 2.7$  for  $\sigma_\alpha = 0.15$  and  $\beta = 0.1$  respectively.

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