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LETTER

How collectively integrated are ecological communities?

Yuval R. Zelnik[1,2] | **Nuria Galiana**[3] | **Matthieu Barbier**[4,5] | **Michel Loreau**[6,7] | **Eric Galbraith**[8,9] | **Jean-François Arnoldi**[6]

[1]Department of Crop Production Ecology, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden
[2]Department of Ecology, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden
[3]Department of Biogeography and Global Change, National Museum of Natural Sciences (CSIC), Madrid, Spain
[4]CIRAD, UMR PHIM, Montpellier, France
[5]PHIM Plant Health Institute, University of Montpellier, CIRAD, INRAE, Institut Agro, IRD, Montpellier, France
[6]Theoretical and Experimental Ecology Station, CNRS Moulis, Moulis, France
[7]Institute of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing, China
[8]Department of Earth and Planetary Science, McGill University, Montreal, Quebec, Canada
[9]Institut de Ciència i Tecnologia Ambientals (ICTA-UAB), Universitat Autònoma de Barcelona, Barcelona, Spain

Correspondence
Jean-François Arnoldi, Theoretical and Experimental Ecology Station, CNRS Moulis, Moulis, France.
Email: jean-francois.arnoldi@cnrs.fr

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Abstract
Beyond abiotic conditions, do population dynamics mostly depend on a species' direct predators, preys and conspecifics? Or can indirect feedback that ripples across the whole community be equally important? Determining where ecological communities sit on the spectrum between these two characterizations requires a metric able to capture the difference between them. Here we show that the spectral radius of a community's interaction matrix provides such a metric, thus a measure of ecological collectivity, which is accessible from imperfect knowledge of biotic interactions and related to observable signatures. This measure of collectivity integrates existing approaches to complexity, interaction structure and indirect interactions. Our work thus provides an original perspective on the question of to what degree communities are more than loose collections of species or simple interaction motifs and explains when pragmatic reductionist approaches ought to suffice or fail when applied to ecological communities.

KEYWORDS
complexity, eigenvalues, holism, indirect interactions, interaction networks, interaction structure, Lotka-Volterra models, press perturbations, reductionism, stability

INTRODUCTION

Ecological communities comprise vast networks of interacting species, which vary greatly in their richness and connectivity (Agrawal, 2001; Brown et al., 2001; Montoya et al., 2006; Pimm, 1984). To understand and predict their behaviour it is tempting to take a reductionist approach, breaking-down complex communities into small parts (predator–prey pairs, competitors within a same niche, etc.). The effectiveness of this approach depends on how accurately knowledge about individual pieces can be scaled up to understand features of the whole. For instance we might hope that, to understand a population's dynamical response to environmental change, it suffices to consider the species' response traits (Lavorel & Garnier, 2002), and to

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Yuval R. Zelnik and Nuria Galiana contributed equally to this work.

a lesser extent the traits of species with which it has strong direct interactions. Given sufficient knowledge and resources, one might also try to consider indirectly connected species at an additional degree of separation. Such an approach would rely on the validity of incremental causality, as we gradually build up a chain of causal links between various interacting units. But a radically different, holistic perspective would be to view a species' response to environmental change as the manifestation of a collective response of the whole ecosystem in which that species is embedded (Patten, 1982).

Explicitly or implicitly, ecologists have argued for decades whether reductionist or holistic perspectives are most appropriate (Loreau, 2020). This debate is often traced back to the opposition, made in regard to plant communities, between the holistic view of Clements and the parsimonious individualistic perspective of Gleason (Lefkaditou, 2012). Clements argued that plant associations should be understood as high-level biological entities, comparable to actual organisms, so that species are best understood through their functions within a whole (Clements, 1916). Gleason claimed that plant communities are mere collections of individual species and gave little importance to the interactions between them (Gleason, 1926). This dichotomy has carried on, with notable ideas such as Lovelock's Gaia theory proposing that the biosphere should be viewed as a super-organism (Lovelock & Margulis, 1974) in profound contrast with the ideas underlying the use of Species Distribution Models that aim to predict species ranges with few key environmental variables (Soberón, 2007).

But there also exists a middle path that simultaneously embraces both reductionist and holistic aspects of ecological communities (Lefkaditou, 2012): to model them as high-dimensional dynamical systems, where variables represent species abundances whose dynamics are coupled by interaction terms. Those interactions are encoded in a matrix so that ecological communities are mapped to a rich class of mathematical objects whose properties can reveal emergent features of the system—that in turn influence the behaviour of its parts (Levins & Lewontin, 1982). Robert May famously showed, using random matrix theory, that stability was virtually impossible past a complexity threshold (May, 1972). This thought-provoking result, contradicting heuristic ideas of their time, opened up a fruitful line of research: looking for interaction structures that allow complex communities to persist (Allesina & Tang, 2015), and thus asking questions about ecological structure and dynamics in terms of matrix features (Novak et al., 2016). In particular, the eigenvalues of an interaction matrix (its spectrum) reveal the dominant modes by which biotic interactions influence population dynamics (Trefethen & Embree, 2020). Whereas eigenvalues of Jacobian matrices determine local stability (Allesina & Tang, 2012; Neubert & Caswell, 1997; Tang & Allesina, 2014), the spectral radius of adjacency matrices reflects the nestedness of bipartite networks (Staniczenko et al., 2013), and from the singular value decomposition of interaction matrices, the likelihood of species coexistence can be derived (Grilli et al., 2017; Rohr et al., 2014). Here, by using such mathematical objects and techniques, we address the reductionist/holistic opposition and show that it can be considered a continuous axis (Liautaud et al., 2019) along which different communities position themselves depending on their complexity and structure (Allesina & Pascual, 2008). We will explain what this positioning tells us about their observable behaviour (e.g. response to perturbations), and discuss how this could be assessed empirically. To do so, we revisit a classic notion of community ecology that may seem unrelated at first: indirect interactions between species (Bender et al., 1984).

The existence of indirect interactions between species indeed challenges the reductionist/individualistic approach to ecological communities (Abrams et al., 1996; Menge, 1995). These interactions are mediated via one or more intermediate populations (Wootton, 1994) and can form long, and numerous, pathways across the community (Puccia & Levins, 2013), generating a multitude of confounding causal pathways between its constituent species. One may think of the feeding chains that couple fungi, bacteria and invertebrates in soil food webs (Neutel et al., 2002) or the indirect interactions between fish and plants via dragonflies whose larvae are eaten by fish and whose adults prey on plant pollinators (Knight et al., 2005). Indirect interactions can couple biomes, determine the loops that control the stability of food webs and impair our capacity to predict a species' response to a given perturbation (Schmitz, 1997; Yodzis, 1988). Indirect interactions thus generate intricate interconnections, leading to emergent community behaviour that is fundamentally different from a collection of populations or isolated interaction motifs (Loreau, 2020).

Here we relate the importance of indirect interaction pathways to the spectral radius of interaction matrices (their largest eigenvalue modulus). Taking a dynamical systems perspective, we compare direct interactions between species pairs to their long-term net interactions (Montoya et al., 2009; Novak et al., 2016; Schmitz, 1997) and then explain how the latter integrates all indirect interaction pathways between them. We demonstrate that the spectral radius of the interaction matrix (once properly normalized by self-regulating forces) determines the length of indirect pathways that contribute to net interactions and thus to long-term community dynamics and patterns. We call this length the "interaction horizon", a notion which mirrors the "environ" concept proposed by Patten (1982) from the era of theoretical ecosystem ecology. As we will see, when interaction horizon diverges, this does not imply unstable behaviour, but the breakdown of incremental causal thinking.

Using simulated communities we illustrate that this interaction spectral radius explains the occurrence of intuitive signatures of collective community behaviour, such as the depth of a perturbation's reach, the degree of temporal unpredictability of a community's response to environmental change or the contribution of biotic processes to realized species niches. We therefore propose the interaction spectral radius as a measure of the degree of collectivity within a community. From spectral radius bounds, in which May's complexity measure plays a central role, we show how to quantify the dynamical role of interaction structures. For instance, in cascade food web models (Pimm et al., 1991), we show that trophic efficiency increases collectivity and so does the nestedness of bipartite (e.g. plant-pollinator) networks (Staniczenko et al., 2013). Our measure of collectivity thus embraces the somewhat disconnected existing approaches to community complexity, interaction structure and indirect interactions.

Overall, our work clarifies when pragmatic reductionist perspectives, focusing on particular species, and small interaction motifs can, at least in principle, be reliably scaled up to the community level, or on the contrary, when there are fundamental obstacles facing such approaches (Bergelson et al., 2021; Orr et al., 2021).

COLLECTIVITY AND THE INTERACTION HORIZON

Here we provide an intuitive introduction to our collectivity parameter, while in Box 1 we give a more formal and general derivation. We then apply those ideas on a simple resource-consumer model.

Our starting point is a community interaction matrix $A = \left(A_{ij}\right)$, with $A_{ii} \equiv 0$. A_{ij} is a non-dimensional number that quantifies the direct interaction of species j on species i. It is crucial to see A_{ij} as a relative interaction strength: the ratio of inter-specific to intra-specific interactions. We emphasize this seemingly technical detail because it is key for properly defining a notion of indirect interactions. If interactions had units, indirect interactions of different orders would themselves have different units, making them incomparable. Studying interaction matrices that have a constant diagonal is commonplace in theoretical ecology, yet it is rarely actually justified (Allesina & Tang, 2012; Jacquet et al., 2016; May, 1972). This property arises naturally when considering relative interaction strength, which for us is a fundamental prerequisite (see Box 1 and example of Equation 6 below).

Following Puccia and Levins (1991) and Neutel et al. (2002), the second-order indirect interaction between species j and i through a third species k is $A_{ik} \times A_{kj}$, the product of the direct interaction of species j on species k with the direct interaction of species k on species i. More generally, an interaction pathway of length n between species i and j is $A_{ik_{n-1}} \times \ldots \times A_{k_2k_1} \times A_{k_1j}$, where the intermediate species $k_1, \ldots, k_n$ need not all be different (loops are possible). Importantly, the sum over all such interaction pathways coincides with the element of A^n:

$$(A^n)_{ij} = \sum_{k_1,\ldots,k_{n-1}} A_{ik_{n-1}} \times \ldots \times A_{k_2k_1} \times A_{k_1j} \tag{1}$$

If all the numbers A_{ij} are strictly smaller than one, the magnitude of indirect interactions will decay exponentially as n grows. Conversely, if the interaction network is sufficiently connected, the number of interaction pathways between species i and j (the number of terms in the sum) will also increase exponentially. It is therefore not clear if the sum of all indirect interactions will necessarily vanish as their order grows, even if direct interactions are individually weak.

To see why Equation (1) will appear in community models, consider the steady-state condition of a Lotka-Volterra system (see Box 1 for a general case):

$$N_i = K_i + \sum_{j=1}^{S} A_{ij} N_j; \quad i = 1, \ldots, S \tag{2}$$

Here K_i—the carrying capacity of species i—has units of biomass and encodes the environmental conditions perceived by that species on its own. If we introduce the vectors $K = \left(K_i\right)$ and $N = \left(N_i\right)$, Equation (2) can be written in compact form as

$$N = K + AN \Leftrightarrow N = (\mathbb{1} - A)^{-1} K \tag{3}$$

Thus the species' intra-specific features K_i intertwine via the matrix $(\mathbb{1} - A)^{-1}$ to determine the actual species abundances in the community context. For instance, a favourable environment (a large K_i) will not imply a large abundance if the environment is also favourable to a competitor. The matrix $(\mathbb{1} - A)^{-1}$ encodes all such effects, that is, all *net interactions* between species. If we had instead repeatedly applied Equation (2) on itself we would have written a series highlighting the contribution of indirect interaction pathways, as defined in Equation (1):

$$N_i = K_i + \underbrace{\sum_j A_{ij} K_j}_{\text{order 1}} + \underbrace{\sum_{j,k} A_{ik} \times A_{kj} K_j}_{\text{order 2}} + \ldots + \underbrace{\sum_{j,k_1,\ldots k_{n-1}} A_{ik_{n-1}} \times \ldots \times A_{k_1j} K_j}_{\text{order } n} + \ldots$$

BOX 1 Direct, net and indirect interactions in stable community models.

Consider a model that specifies the growth rate g_i of all species, as a function of their joint abundances $\boldsymbol{N} = \left(N_i\right)$:

$$\frac{1}{N_i}\frac{dN_i}{dt} = g_i(\boldsymbol{N}) \tag{13}$$

In Generalized Lotka-Volterra (GLV) models $g_i(\boldsymbol{N}) = r_i + \sum_j a_{ij} N_j$, with $a = \left(a_{ij}\right)$ representing per-capita interactions and $\boldsymbol{r} = \left(r_i\right)$ the vector of species intrinsic growth rates. We assume that the community is in a steady state $\boldsymbol{N}^*$, so that $g_i\left(\boldsymbol{N}^*\right) = 0$. In that state, we want to define direct and net species interactions, relate them to one another and show *in what sense net interactions emerge as a sum of indirect* ones, a claim that we use to quantify the collective integration of the community.

Direct interactions reflect the sensitivity of the growth rate of one species, to a change in abundance of another. In mathematical terms, this amounts to defining the matrix of partial derivatives

$$\frac{\partial \boldsymbol{g}}{\partial \boldsymbol{N}} := \left(\frac{\partial g_i}{\partial N_j}\right) \tag{14}$$

which for GLV models, coincides with the matrix $a = \left(a_{ij}\right)$.

Net interactions *are the reciprocal of direct interactions*: the long-term sensitivity of the abundance of a species, to a permanent shift in the growth rate of another (Montoya et al., 2009; Novak et al., 2016). In matrix form, net interactions can be written as

$$\frac{\partial \boldsymbol{N}^*}{\partial \boldsymbol{g}} := \left(\frac{\partial N_i^*}{\partial g_j}\right) \tag{15}$$

To clarify the meaning of Equation (15), imagine applying a small press perturbation $\delta\boldsymbol{g}$ on the species' growth rates. In contrast with the way direct interactions are defined, we now *let community dynamics play out*, ultimately leading to a shift in equilibrium abundances $\delta\boldsymbol{N}^*$, so that

$$\boldsymbol{g}\left(\boldsymbol{N}^* + \delta\boldsymbol{N}^*\right) + \delta\boldsymbol{g} = 0 \Leftrightarrow \frac{\partial \boldsymbol{g}}{\partial \boldsymbol{N}} \cdot \delta\boldsymbol{N}^* + \delta\boldsymbol{g} = 0 \tag{16}$$

This expression can be inverted to show that the matrix of net interactions is indeed the inverse of the matrix of direct interactions:

$$\frac{\partial \boldsymbol{N}^*}{\partial \boldsymbol{g}} = \left(-\frac{\partial \boldsymbol{g}}{\partial \boldsymbol{N}}\right)^{-1} \tag{17}$$

In GLV models this matrix also determines the steady state $\boldsymbol{N}^* = \left(-a^{-1}\right) \cdot \boldsymbol{r}$.

Indirect interactions and the collectivity parameter. Direct and net interactions have reciprocal units. Furthermore, if we multiply the direct interaction between species i and j, with the direct interaction between species j and k, this would change dimensions and define an indirect interaction between species i and k that cannot be compared to neither direct nor net interactions. However, by defining direct interactions *relatively to self-regulation*, defined for any species i as $-\frac{\partial g_i}{\partial N_i}$, we can revisit the connection between direct and net interactions such that a coherent notion of indirect interaction emerges. Let direct, *non-dimensional* interactions be

$$A_{ij} := \frac{\partial g_i}{\partial N_j} \Big/ \left(-\frac{\partial g_i}{\partial N_i}\right); \quad i \neq j; \quad \left(A_{ii} = 0\right) \tag{18}$$

In GLV models this corresponds to $A_{ij} := a_{ij} / \left(-a_{ii}\right)$. If D is the diagonal matrix encoding species self-regulation, and $\mathbb{1}$ the identity matrix, direct interactions can be written as

$$\frac{\partial \boldsymbol{g}}{\partial \boldsymbol{N}} = D \cdot \underbrace{\left(-\mathbb{1} + A\right)}_{\text{non} - \text{dimensional} \quad \text{direct} \quad \text{interactions}} \tag{19}$$

Box 1 (Continued)

which indeed have the same units as D. From Equation (17), it follows that

$$\frac{\partial \mathbf{N}^*}{\partial \mathbf{g}} = \underbrace{(\mathbb{1}-A)^{-1}}_{\text{non-dimensional net interactions}} \cdot D^{-1} \tag{20}$$

If the elements of A are small, the *non-dimensional* net interaction matrix $(\mathbb{1}-A)^{-1}$ can then be written as a convergent infinite series

$$(\mathbb{1}-A)^{-1} = \mathbb{1} + A + A^2 + \ldots \tag{21}$$

This series enables us to define indirect interactions of order k as the elements of A^k. Indeed $\left(A^k\right)_{ij}$ is the sum of all non-dimensional interaction pathways of length k that lead from species j to i (allowing for loops), drawn in the interaction network. Those should not be confused with higher-order interactions (Battiston et al., 2021), which are defined as non-linear interaction terms in community models (see discussion in Supporting Information S4). It is in the precise sense of Equation (21) that net interactions emerge as a sum of indirect ones. Our measure of collectivity ϕ is the spectral radius of A (Trefethen & Embree, 2020), namely:

$$\phi = \max\{|\lambda|;\ \ \lambda \in \mathrm{spect}(A)\} \tag{22}$$

which controls the rate of convergence of the series Equation (21) and thus the order of indirect interactions that contribute to net interactions.

Since this last expression should be equivalent to Equation (3), and for all vectors K, we arrive at a classic matrix identity, known as Neumann's series (Reed et al., 1972),

$$\mathbb{1} + A + A^2 + \ldots + A^n + \ldots = (\mathbb{1}-A)^{-1} \tag{4}$$

This series converges only under some specific conditions. When it does not converge, this means that we cannot meaningfully decompose net interaction as a sum of indirect interaction pathways.

The criteria for convergence gives us both a measure of the importance of indirect interactions and a *definition* of collective integration. To derive this criteria, we first need to measure the magnitude of the various terms of the series, representing the overall strength of indirect interactions of all orders. This amounts to defining a matrix norm for each term $\| A^n \|$, and see how this norm changes with the order n. Consider

$$\phi = \lim_{n\to\infty} ||A^n||^{1/n}, \tag{5}$$

that is, the rate of growth of the norm $\| A^n \|$ as n grows. If $\phi < 1$, as n grows, the overall contribution of indirect pathways will *eventually* decrease exponentially as ϕ^n. If $\phi > 1$, the sum over arbitrarily long pathways can be arbitrarily large (cf. Figure 1).

Remarkably, ϕ does not depend on the particular choice of matrix norm. It is an intrinsic feature of the interaction matrix A: its spectral radius, the largest absolute value of its eigenvalues (Trefethen & Embree, 2020).

Here we propose an ecological interpretation of the spectral radius ϕ of a given interaction matrix. We call ϕ the *collectivity parameter* because it determines the *interaction horizon* of species: the maximal length of interaction pathways that contribute to their net interactions (see Figure 1). For systems for which $\phi > 1$, the interaction horizon is infinite, signalling the breakdown of the reductionist method of decomposing net effects into indirect interaction pathways, which we see as a reflection of the highly collective integration of such communities.

Example: We illustrate how the preceding ideas play out in a simple resource-consumer model (see Supporting Information S1 for a generalization). Let N_C and N_R be the abundance of consumer and resource, respectively, which are assumed to follow, as in Galiana et al. (2021):

$$\begin{aligned} \frac{1}{N_C}\frac{dN_C}{dt} &= -d_C N_C + \epsilon\alpha N_R - m \\ \frac{1}{N_R}\frac{dN_R}{dt} &= -\alpha N_C - d_R N_R + r \end{aligned}$$

Here $d_{C,R}$ represent intra-specific interactions, α is the attack rate and ϵ is trophic efficiency, while m and r are intrinsic mortality and growth rate of both species. Following the general derivation of Box 1, the non-dimensional interaction matrix is

$$A = \begin{pmatrix} 0 & \varepsilon a \\ -a & 0 \end{pmatrix};\ \ \varepsilon = \epsilon d_R / d_C;\ \ a = \alpha / d_R \tag{6}$$

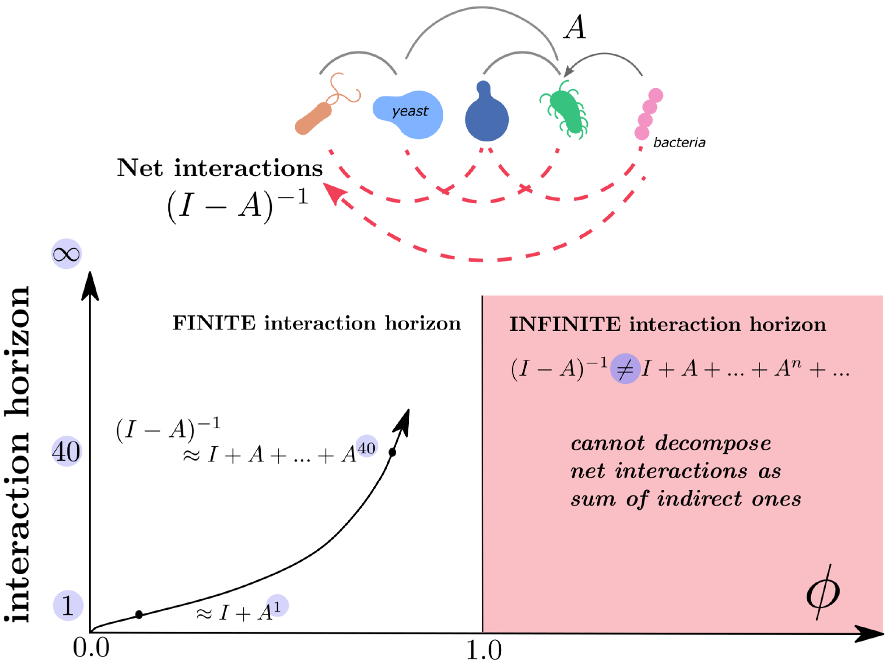

FIGURE 1 The interaction horizon is the maximal length of indirect interaction pathways that substantially contribute to net interactions (illustrated here in a hypothetical yeast-bacteria community). The horizon is directly determined by the collective parameter as $\log\epsilon / \log\phi$, where $\epsilon < 1$ is an arbitrary threshold value. The horizon gives the lowest order of interactions for which the maximal contribution is negligible (i.e. smaller than ϵ), and it diverges as ϕ approaches 1. Beyond this point it no longer makes sense to decompose net interactions as a sum of indirect pathways.

This matrix has purely imaginary eigenvalues $\pm ia\sqrt{\epsilon}$ so that the collectivity parameter is $\phi = a\sqrt{\epsilon}$, proportional to the attack rate. Because eigenvalues are imaginary, stable steady states exist[1] for any values of ϕ. The inverse matrix—which determines net interactions—can be written in terms of ϕ:

$$(\mathbb{I} - A)^{-1} = \frac{1}{1+\phi^2}\begin{pmatrix} 1 & \phi\sqrt{\epsilon} \\ -\phi/\sqrt{\epsilon} & 1 \end{pmatrix}$$

The net interaction between resource and consumer is thus proportional to $\phi/\left(1+\phi^2\right)$. This non-monotonous function of ϕ (and thus of attack rate) increases until $\phi = 1$, before decreasing. We deduce that at high collectivity, net and direct interactions become anti-correlated. This counter-intuitive phenomenon cannot be understood when considering only a few, albeit long, indirect interaction pathways because such a decomposition would only converge in the phase where net and direct interactions go hand in hand.

THREE SIGNATURES OF COLLECTIVE INTEGRATION

We now introduce three signatures of collective integration, which could conceivably be observed empirically. Not all three would be indicative of collectivity in a given system, but taken together they apply to a broad spectrum of ecological scenarios. We look for those signatures on a set of Generalized Lotka-Volterra (GLV) model communities, taken in a steady state following community assembly from a random species pool.

In simulations we consider a gradient y of interaction strength (and heterogeneity), with 50 different values of overall interaction strength between 0.02 and 1, each with 100 random communities, making 5000 communities in total. Each starts from a pool of $S = 50$ species, and we set 80% of interactions to zero to have sparse interaction networks. To parameterize interaction strength, we follow May (1972), Allesina and Tang (2012), Bunin (2017) and Barbier et al. (2018) and define three parameters of random interactions: $\mathrm{std}\left(A_{ij}\right) = y/\sqrt{S}$; $\mathrm{mean}\left(A_{ij}\right) = -y/S$; and $\mathrm{corr}\left(A_{ij}, A_{ji}\right) = -1$. This leads to anti-correlated interactions between species that are increasingly negative and varied. In this way we could generate communities with a collectivity parameter ϕ ranging between 0 and ~ 2, which we use to showcase generic aspects of low and high collective integration in species-rich communities.

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[1] The Jacobian matrix that controls near-equilibrium dynamics reads $J = D_N(-\mathbb{I} + A)$, where D_N is a diagonal matrix whose entries are $d_{C,R}N^*_{C,R}$, and $N^*_{C,R}$ are the species equilibrium values. Stability requires that eigenvalues of J have negative real part. Here we only know that eigenvalues of $-\mathbb{I} + A$ have negative real part, but we can always adjust the positive factor D_N, by modifying r and m, so that it will not change the sign of eigenvalues.

Details about simulations and an additional signature (that we call "growth of effective connectance") are given in Supporting Information S5 and S6.

Perturbation depth

Collective integration means that species are interdependent so that a perturbation targeted on a given species will likely propagate deep into the community (Bender et al., 1984). Experimentally one could remove a species, and monitor the responses of others, as a function of their interaction distance $d(i,j)$ from the removed species ($d(i,j) = 1$ if j interacts with i, $d(i,j) = 2$ if i and j are indirectly connected via a third species, etc.). Denoting $N_{j\setminus i}$ the long-term abundance of species j after removal of species i, one can quantify *perturbation depth* as

$$\mathrm{PD} = \frac{\sum_j d(i,j)\left|N^*_{j\setminus i} - N^*_j\right|}{\sum_j \left|N^*_{j\setminus i} - N^*_j\right|} \tag{7}$$

which we can average over all species removal experiments in that community.

In Figure 2a we demonstrate a good agreement between this observable signature of collective integration and the collectivity parameter ϕ. As collectivity grows, the brunt of the perturbation effect is shared with more distant species, and not only supported by those directly in contact with the removed node (Figure 2b). An obvious caveat of perturbation depth is that it only applies to sufficiently sparse networks – if all species are connected, this notion is not well defined. We show in Supporting Information S6.2.1 how this limitation can be overcome, by defining a distance function $d(i,j)$ that is based on the quantitative values of interaction.

Temporal unpredictability

Indirect interactions between species require time to take effect. Thus, collective integration is expected to leave a signature in the relationship between short- and long-term responses to a perturbation. Following a persistent change in abiotic conditions, a given species' population will first react to the induced change in its intrinsic growth rate. Later, direct interactions between species will take effect, followed by longer interaction pathways. However, if the strength of indirect interactions rapidly decays with their length, the latter will not substantially change the population dynamics; the long-term outcome could have been extrapolated from the short-term response. Therefore, the more collectively integrated the community, the less predictable the long-term response of a species should be.

We test this idea by randomly perturbing the intrinsic growth rates of all species of a community at equilibrium. We then measure the correlation between a vector of short-term response extrapolation R_S and a vector of the actual long-term response R_L (Supporting Information S6.3) and define temporal unpredictability as the complement of that correlation:

$$\mathrm{TU} = 1 - \mathrm{corr}\left(R_S, R_L\right) \tag{8}$$

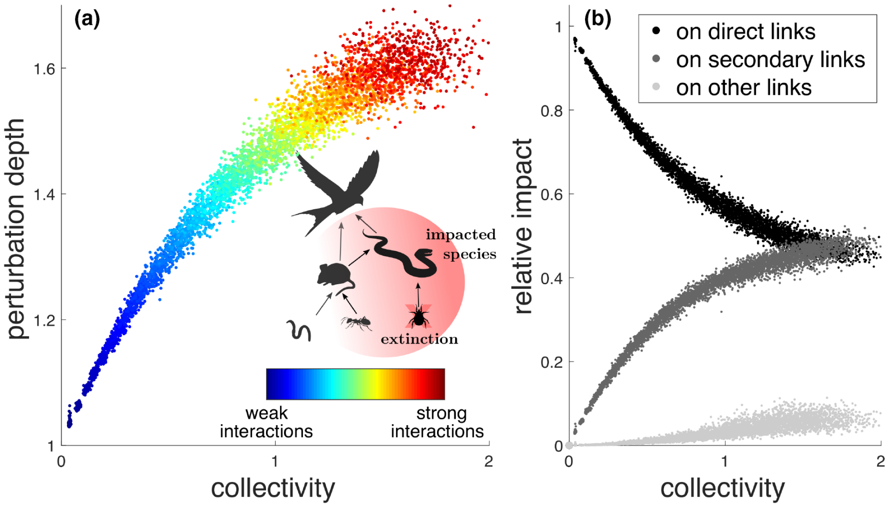

FIGURE 2 Perturbation depth and collectivity. For various communities, the effect of removing a single species is seen across the community. Panel (a) shows the perturbation depth, a measure of how deep into the network of species interactions does the perturbation reach. Panel (b) shows the average effect on the species in the community (all except the one species removed), partitioned into three groups: black for species directly interacting with removed species, dark grey for species directly interacting with the species in the black group, light grey for all other species. As collectivity increases the average effect on a given species becomes equal, regardless of its grouping (i.e. its position in the community structure), and therefore the perturbation depth increases (i.e. the effect of the perturbation if felt throughout the community). Details about simulation procedure can be found in Supporting Information S5.

In Figure 3 we see temporal unpredictability increasing steadily with collectivity ϕ, meaning that trajectories can change tendencies through time, as indirect interactions come into play (right panel). Here too there is a caveat. If direct interactions are mediated by slow latent variables, such as unobserved species or modified environmental variables, time and length of interaction pathways need not be related. Collectivity thus leaves an unambiguous signature in temporal trends only if a separation of time scales exists between the factors that mediate direct interactions and the actual population dynamics.

Biotic contribution to the realized niche

If species do not interact, only the abiotic environment (i.e. what cannot be attributed to the rest of the community) determines the species' growth and abundance. In general, however, species change the environmental conditions perceived by other species. Intuitively, we expect stronger collective integration when this biotic contribution is more important and intricate (Levine et al., 2017).

To quantify this collective contribution, we start from the relative yield of a given species, $\eta_i = N_i / K_i$. This amounts to comparing mono-cultures to polycultures (second column of Figure 4). The absolute difference between relative yield and unity is a measure of the net effect, on species i, of the biotic environment. We measure this effect integrated over the community, and to make the result comparable across communities, we normalize by the sum of relative yields. This defines a measure of the biotic contribution to species realized niches:

$$\mathrm{BC} = \frac{\sum_i (\eta_i - 1)^2}{\sum_i \eta_i^2} \tag{9}$$

which is similar to the relative Euclidean distance $\| N - K \| / \| N \|$ between the realized community state N (expressing the realized niche) and what it would have been without interactions, K (the fundamental niche).

We can also characterize the raw contribution of the biotic environment by comparing the realized abundance of species to those achieved if species had the same carrying capacity (third column of Figure 4). In fact, this amounts to asking how much a species abundance is explained by its *centrality* in the interaction network (Sharkey, 2017).

In the first panel of Figure 4, we see that the collectivity parameter and the strength of the biotic niche Equation (9) closely follow one another. For communities with collectivity parameter close to or larger than 1, species abundances are not at all explained by the abiotic environment, but instead are almost entirely controlled by the biotic environment set by the whole community. The caveat here is the requirement of a notion of carrying capacity, which makes sense for, say, plants but is ill-defined when considering consumer species.

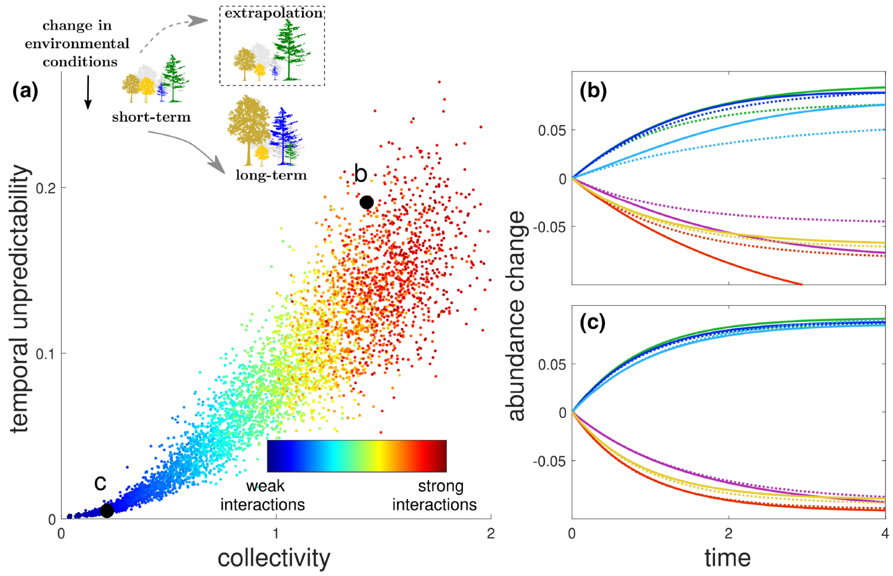

FIGURE 3 Temporal unpredictability between short-term and long-term responses to perturbation. For various communities, the ability to predict the long-term response of a community to a perturbation from its short-term response is evaluated and shown. Panel (a) shows temporal unpredictability, which gives a score of 0 for a perfect correspondence between short-term and long-term responses. Black circles show the collectivity and temporal unpredictability for two communities, with the corresponding dynamics shown in the right panels (b) and (c). Right panels show the change in abundance for six species in each community, where the dashed lines show the extrapolated dynamics based on the short-term fit (using the first 0 to 0.5 time units), whereas the solid lines show the actual dynamics. With higher collectivity the long-term behaviour becomes less predictable. Details about simulation procedure can be found in Supporting Information S5 and S6.

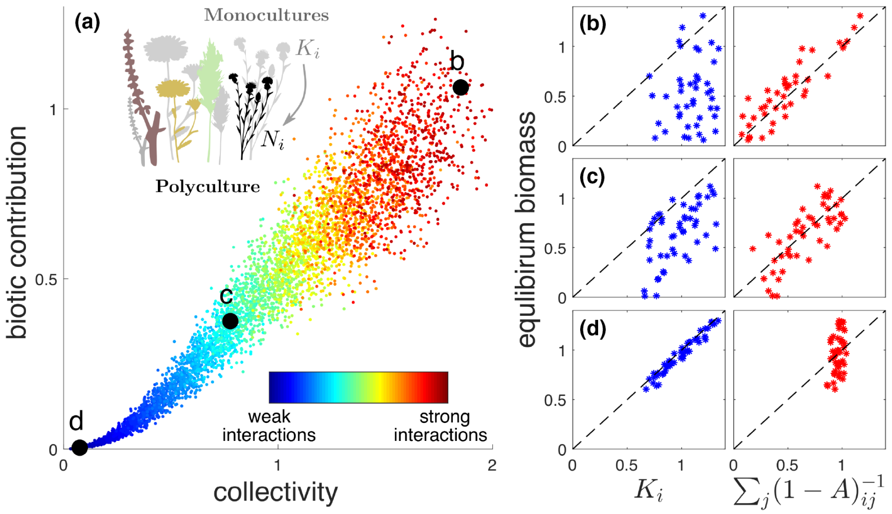

FIGURE 4 Biotic contribution to species realized niches. The determinants of the community's species abundance at equilibrium are evaluated. (a) The biotic contribution to the realized niche (Equation 9), with black circles highlighting several communities that are considered in the right panels. (b)–(d) Species equilibrium abundance for different communities (corresponding to black circles in panel a), compared with its carrying capacity (left in blue), or by contrast, with its abundance if all species had the same carrying capacities so that differences in abundances are caused by species interactions only (on the right in red). Dashed black line shows the 1:1 line. Details about simulation procedure can be found in Supporting Information S5 and S6.

COLLECTIVITY, COMPLEXITY AND STABILITY

In this section we relate collectivity to the *complexity* measure of May (1973), which we then use to assess the role of network structure and discuss the sensitivity of collectivity to uncertain knowledge of biotic interactions. We will also clarify similarities and differences between collectivity and the widely studied notion of asymptotic *stability*.

We first invoke known properties of the spectral radius to deduce useful bounds on collectivity. By definition, $\phi \le \|A\|$, where $\|A\|$ is the spectral norm of A, the maximal amplification of vectors' length that this matrix can achieve (Reed et al., 1972; Trefethen & Embree, 2020). The spectral norm is related to a simpler norm, via the following general equivalence relation (Reed et al., 1972):

$$\sqrt{1/S}\|A\|_F \le \|A\| \le \|A\|_F \tag{10}$$

where $\|A\|_F$ is the Frobenius norm of A: the square root of the sum of squared elements of A. Thus, $\sqrt{1/S}\|A\|_F$ is really $\sqrt{S\left\langle A_{ij}^2\right\rangle}$, with $\left\langle A_{ij}^2\right\rangle$ the mean of squared interactions (accounting for the trivial diagonal terms $A_{ii} \equiv 0$). We can develop this term a little more by introducing the network's connectance $0 \le p \le 1$ (i.e. the proportion of realized links) and ξ^2 the second moment of interactions between connected species, so that

$$\sqrt{1/S}\|A\|_F = \sqrt{S\left\langle A_{ij}^2\right\rangle} = \sqrt{p(S-1)\xi^2} \equiv C, \tag{11}$$

in which we recognize C, the complexity measure introduced by May (1972) in his seminal work on Random Matrix Theory and the complexity-stability debate (McCann, 2000).

Finally, given that $A_{ii} \equiv 0$, we can transform the general equivalence relationship Equation (10) to deduce a similar relationship between complexity and the spectral radius of interaction matrices (Supporting Information S1):

$$C = \phi_{low} \lesssim \phi \le \phi_{up} = C\sqrt{S-1} \tag{12}$$

The upper bound ϕ_{up} is sharp[2] while the lower bound ϕ_{up} is an approximation (only sharp for normal matrices). Because they do not depend on the way interactions are actually distributed across species, those bounds can be used to quantify the role of structure. Rescaling ϕ as $(\phi - \phi_{low})/(\phi_{up} - \phi_{low})$ defines a measure of relative collectivity for which a value of 1 means that the upper bound is reached, indicating that structure maximizes collectivity, while a value of 0 implies that ϕ is unaffected by randomizing interaction terms. In Supporting Information S1 and S2 we provide examples of structures, from competitive networks to food-web models, that greatly affect collectivity, allowing to move from one bound to the other.

The lower bound ϕ_{low} in Equation (12) should be seen as the collectivity that "comes for free" if the

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[2] For instance, ϕ is equal to the upper bound in a competitive network where competition strength is uniform across species (Supporting Information S1).

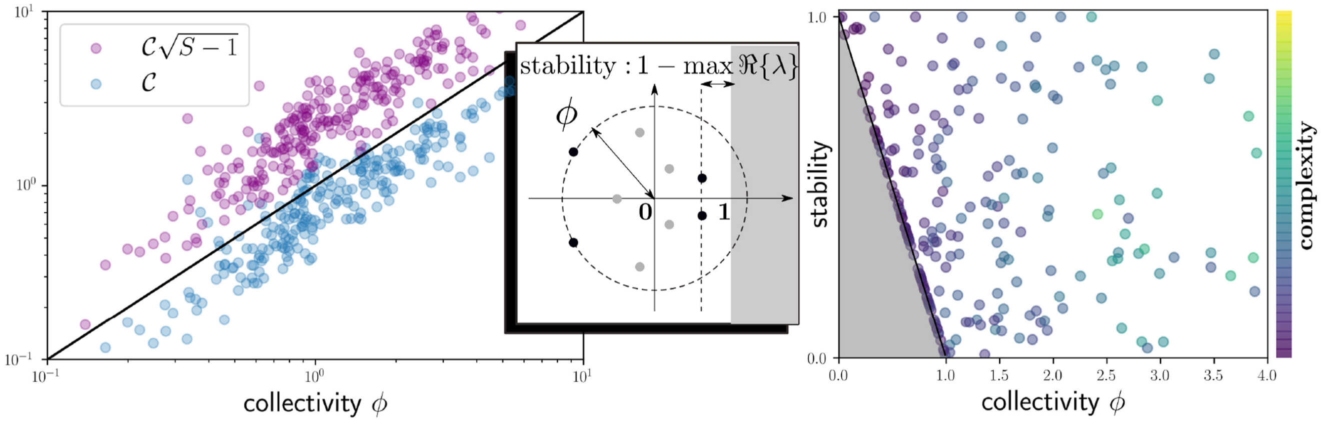

FIGURE 5 Left: May's complexity $\mathcal{C}$ sets the bounds of collectivity, illustrated here for 242 random stable matrices (out of 1000 generated) of size 5×5 to 15×15, representing interaction matrices A of various connectance, interaction strength, variance and pairwise symmetry (notice the log–log scales). In purple the sharp upper bound $\mathcal{C}\sqrt{S-1}$ where S is the size of the community (purple points are always above the one:one line in black). In blue is the approximate lower bound $\mathcal{C}$ (blue points mostly remain below the one:one line). Middle inset: Stability is here a distance to instability $1 - \max\Re\{\lambda\}$, where $\max\Re\{\lambda\}$ is the maximal real part over all eigenvalues $\lambda \in \mathbb{C}$ of the interaction matrix. If this real part attains 1, the community is unlikely to be stable—shaded region is the instability domain. Collectivity is instead the radius of the smallest disc centred on 0 that contains all eigenvalues. Right: collectivity and (in)stability are not equivalent. Same matrices as on the left panel. We see that large values of collectivity are allowed even if we restrict to stable systems. The edge of the grey region represents $y = 1 - x$ which is what would be expected if collectivity and stability were associated with the same eigenvalue.

matrix was random, but non-random structure can reduce collectivity far below this baseline. Furthermore, this baseline expectation can be refined to account for additional statistical features of interactions, such as their mean and variance. In fact, the spectral description of large random matrices given by Allesina and Tang (2012) directly gives a random matrix prediction for ϕ that accounts for interaction mean, variance and also pairwise correlation (Supporting Information S2.1). The accuracy of this prediction, which we test in Figure S3, demonstrates that, in the absence of a clear structure, collectivity can be reliably estimated using only summary statistics of interactions. In Supporting Information S2.2 we test this claim by estimating collectivity from incomplete knowledge of interactions. Concretely, we assume accurate knowledge of only a fraction of interactions, while the rest are inferred from the statistics of the measured ones. In the absence of structure this procedure generates good predictions for ϕ. In fact, any method that can infer interaction statistics, without necessarily providing any reliable information about individual interaction terms, would still give an accurate approximation of collectivity. However, if an underlying structure exists in the network, so that collectivity is far from the baseline, random, expectation, basic statistics of interaction strength are insufficient. They must be combined with knowledge of structural features (Asllani et al., 2018). In Supporting Information S2.2 we illustrate this idea using a cascade food-web model (Pimm et al., 1991), where predators feed on smaller species. The trophic structure generates a substantial departure from the random baseline. However, given basic features of this structure, only summary statistics of attack rate and trophic efficiency are required to accurately predict the food web's degree of collectivity.

Finally, if ϕ is associated with May's complexity measure, should it not be directly related to stability, at least sensu May (1972)? The linear stability criterion is that all eigenvalues of the Jacobian matrix at the steady state must have a negative real part (Lyapunov, 1892). This is essentially[3] equivalent to all eigenvalues of A having a *real part* smaller than 1 (Gibbs et al., 2018). Collectivity ϕ is instead the largest eigenvalue *modulus*. As is made clear once represented graphically (see middle inset of Figure 5), if the system is unstable, ϕ is necessarily larger than 1. However, even if ϕ is large, the real part of the associated eigenvalue can still be arbitrarily small (this is the case in the consumer-resource model of equation 6). So instability implies a high degree of collective integration *but the converse is not true*. Large collective integration does not necessarily imply instability (right panel of Figure 5).

DISCUSSION

In this theoretical piece, we have addressed two interlinked issues, which are both of conceptual and practical importance: (i) how to bridge between reductionist and holistic conceptions of ecological communities,

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[3] The Jacobian matrix can be written as $J = D_N(-\mathbb{I} + A)$, the product of a *positive* diagonal matrix D_N that contains species abundances at steady state and their intra-specific interaction strength, times our non-dimensional interaction matrix. In general J and $-\mathbb{I} + A$ will not have the same eigenvalues, but because D_N is diagonal and positive, it is unlikely (although not impossible) that some eigenvalues' real parts become positive when going from $-\mathbb{I} + A$ to J (Gibbs et al., 2018).

with a well-defined quantitative axis, and (ii) how to better understand and quantify the dynamical role of interaction structure. These two points go back to two classic dichotomies of ecology: reductionist versus holistic views and dynamics versus structure. They are also practical. Point (i) clarifies when we can hope to predict behaviour using incremental causality. Point (ii) helps us understand community dynamics even with limited data.

The premise of our work is that, in nature, dynamical inter-dependency between species occurs not only through direct interactions, via predation, facilitation or competition, but through potentially much longer indirect interaction pathways (Wootton, 1994). When long indirect pathways significantly contribute, over relevant time scales, to population dynamics, the state of a species can depend on many—if not all—other species in the community. We hypothesized that in such instances, the incremental causal thinking that characterizes individualistic approaches would become misleading (Levins, 1974). We also expected that when contributing interaction pathways are long, perturbations propagate further; that short-term and long-term responses of species become uncorrelated; and that in such collectively integrated communities, it is the biotic environment (and not the abiotic one) that dominantly shapes abundance distribution patterns.

Taking a dynamical systems perspective on ecological communities led us to study the spectral radius ϕ of a community's interaction matrix (Novak et al., 2016), defined as its largest eigenvalue modulus (Reed et al., 1972). Indeed, we showed that in dynamical models, it is this precise feature of the set of interactions that determines the length of non-negligible indirect interactions (cf. Box 1). Moreover, we explained that when the spectral radius ϕ is greater or equal to 1, arbitrarily long interaction pathways can have, over large time scales, as much importance as short ones. It then becomes impossible to decompose long-term effects as a sum of dominant direct or indirect interaction pathways. In this sense, incremental causality breaks down.

We proposed to see ϕ as a measure of collective integration, as it drives empirically relevant collective behaviour. On simulated ecological communities, we demonstrated that ϕ drives *Perturbation depth*, defined as the network distance covered by perturbations initially affecting only a single species. We also showed that ϕ increases *Temporal unpredictability*, defined as the discrepancy between species' long-term behaviour after a change in environmental conditions and the extrapolation of their dynamics based on their short-term response. We finally related the value of the collectivity parameter with a measure of *Biotic contribution* to species realized niches, defined to quantify the degree to which abundances of species grown in monocultures fail to predict the abundances of those same species when grown together.

We then showed that our measure of collectivity parameter is controlled by the complexity measure of May (1972), a summary statistic of absolute interaction strength between species. Complexity, together with species richness, determines both an upper bound on collectivity and a baseline expectation. Thus complexity sets the baseline for collectivity, while the interaction structure determines how much it will depart from the baseline, either reducing collectivity or increasing it towards the upper bound. We identified structures that push towards maximal collectivity, such as evenly distributing interactions or increasing pairwise symmetry. By contrast, triangular (i.e. hierarchical) structures, because they buffer feedback (Tilman, 1994), drastically reduce collectivity. In Supporting Information S2.2 we consider a cascade food web model (Pimm et al., 1991), to show that trophic efficiency, which determines how predators utilize prey biomass, is a major structural driver, making food webs go from low collectivity when efficiency is low to near-maximal values for high efficiency.

In a similar vein, Staniczenko et al. (2013) used the spectral radius of adjacency matrices to quantify the nestedness of bipartite interaction networks,[4] where one group of species interacts with another group (e.g. plants and pollinators). In their work, links can be weighted and not just binary (using frequency of insect visit per plants for instance). However, the spectral radius of such weighted adjacency matrices should not be seen as a measure of collectivity, as the latter depends on the ratio of inter-specific to intra-specific interactions (in the precise sense given in Box 1). Nonetheless, we can still compare the spectral radius with the random baseline and its upper bound (Chung, 1997), to see which structures favour collective behaviour, those that have no effects, and those that ought to reduce it. Given that Staniczenko et al. (2013) find that nestedness is associated with a higher than expected spectral radius, we may say that, ceteris paribus, nestedness favours collective behaviour in bipartite communities.

Overall, our work provides a novel perspective on ecological network structure: instead of asking whether biotic structures tend to make communities more or less stable (May, 1972), we can now ask whether those structures tend to make communities more or less collectively integrated than if they had been randomly assembled.

Long indirect pathways between species, whose importance unfolds over variable time scales, do not favour predictive power. As previously shown (Barabás et al., 2014; Schmitz, 1997; Yodzis, 1988, 2000), this is certainly true if one tries to predict the effect that a perturbation will have, in the long term, on a given species when the latter is embedded in a complex

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[4] Plant-pollinator networks are often nested: specialist insects typically pollinate a subset of the plants pollinated by generalist species.

ecosystem. But this typical sensitivity of individual variables need not imply that all properties of a community or ecosystem are sensitive and/or unpredictable (Daugaard et al., 2022). We know, in particular, that many aggregate features of complex models are robust to uncertainty in parameters (Barbier et al., 2018). Our work can help identify cases in which long indirect interaction pathways cannot be ignored or even simply added up. In such instances we must change perspective and focus our efforts towards robust ecosystem or community-level properties of the natural system under study (Bergelson et al., 2021; Goldford et al., 2018; Sanchez et al., 2023).

Perspectives

Contrary to the dynamical community models we studied, real communities are open to migration, structured spatially and neither deterministic nor stable (Hastings, 2004). It is not obvious how to translate our analysis of ecological collectivity to transient, far from equilibrium dynamics or draw conclusions on the role played by spatial structure and scale in determining the degree of collective integration of ecological systems. For the latter, this relates to the meta-community concept (Holyoak et al., 2005) and the quest to better understand the spatial scaling of ecological interactions (Galiana et al., 2018, 2022; Gravel et al., 2016). This is a promising direction that could help better formulate the scale transitions of ecological patterns, as it is commonly thought that at large scales, ecological systems are mostly determined by abiotic drivers, thus suggesting a negative collectivity-scale relationship. On the issue of considering transient states, powerful dynamical techniques do exist to tackle transients in complex systems (Roy et al., 2019). But even without abandoning the notions of stationarity or equilibria, we could expand our formalism to address the time-scale dependency of collectivity. A way forward may be the study of power spectra of ecological time series: decomposing the temporal fluctuations of populations over various time scales to infer the interaction structures that generate such signals (Krumbeck et al., 2021). Here we suspect that variations over longer time scales reflect the collective nature of communities more than those at much shorter time scales, as the latter would not allow for indirect interactions to manifest, as seen in Figure 3.

Finally, can we measure the degree of collective integration in empirical data? The fact that collectivity is controlled by aggregate interaction statistics (see Figure 5) means that we need not precisely measure all species interactions to estimate collectivity bounds. In fact, basic interaction statistics entirely determine collectivity in the absence of structure (Allesina & Tang, 2012), which can allow its estimation from incomplete or noisy interaction strength data (Supporting Information S2.1). But more generally, we can expect that there will often exist a combination of basic aggregate features of structure and interaction strength that drive our measure of collectivity. For instance, in the food-web model example shown in Supporting Information S2.2, basic topological structure, mean attack rate and trophic efficiency are the main drivers. This is reassuring as any theoretical notion that is sensitive to fine scale details is guaranteed to be irrelevant. That being said, can we reliably estimate collectivity from, say, time-series analysis (Sugihara et al., 2012) or residual correlations in species distributions (Ovaskainen & Abrego, 2020)? In Supporting Information S2.3, we give a proof of concept for the latter, showing that in unstructured competitive communities, collectivity is surprisingly well estimated from the correlation between species abundances across environments. Developing such ideas could be a realistic way forward towards quantifying the dynamical importance of biotic interactions in complex communities.

AUTHOR CONTRIBUTIONS

YZ, NG and JFA designed the study. YZ performed numerical simulations, JFA derived mathematical results. YZ, NG and JFA wrote the manuscript with feedback from all authors.

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DATA AVAILABILITY STATEMENT

The manuscript contains no data. The computer code used for the simulations is found at the open-access repository: https://doi.org/10.5281/zenodo.7537451.

ORCID

Yuval R. Zelnik https://orcid.org/0000-0002-9748-8756
Nuria Galiana https://orcid.org/0000-0001-7720-0615
Matthieu Barbier https://orcid.org/0000-0002-0669-8927

Michel Loreau https://orcid.org/0000-0002-0122-495X
Jean-François Arnoldi https://orcid.org/0000-0001-9373-4051

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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