

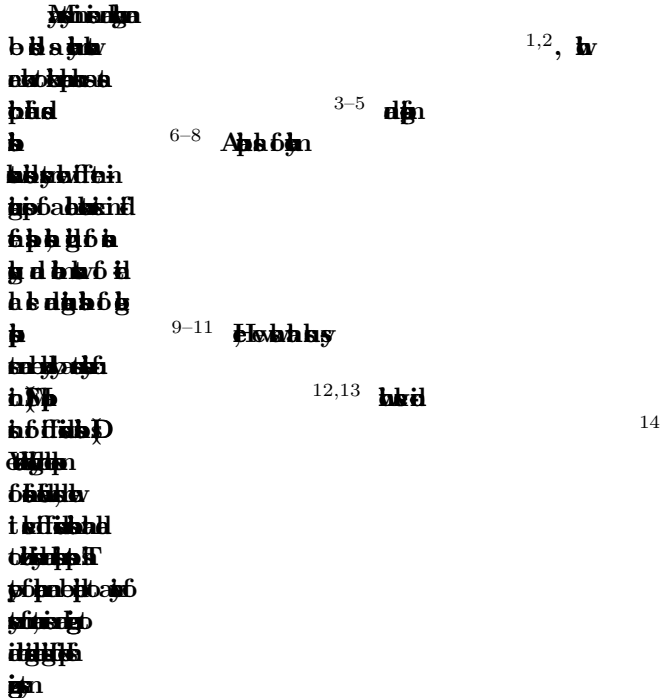
# Master stability functions reveal diffusion-driven instabilities in multi-layer networks

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Understanding the dynamics of multi-layer networks is difficult because of the number of variables in these systems and the complex structure of their interactions. The key challenge is therefore to leverage multi-layer structure in the analysis. Previous approaches used network measures to quantify structure<sup>1,15,16</sup> and percolation theory to understand cascades.<sup>3-5</sup> Particularly for meta-foodwebs discrete-state colonization-extinction models were analyzed.<sup>17,18</sup> However, less progress has been made in multi-layer networks with continuous-time dynamics. Recent works<sup>6,7,19</sup> revealed the existence of DDIs in 2-layer systems. The main difficulty that impedes the analysis of larger systems is the size and complexity of the system's Jacobian matrix, a central object in stability analysis. To overcome this difficulty, inspiration can be drawn from dynamics in continuous space: Here, it is possible to decompose the local dynamics into eigenfunctions of the spatial domain.<sup>14,20</sup> Stability of the spatial system is then captured by almost the same Jacobian matrix that describes the stability of an

isolated system, where the effects of space only appear as a minor modification. This reduction in complexity is possible because the approach exploits the homogeneity of the underlying space. In networks, a similar reduction is achieved in the MSF approach to oscillators dynamics.<sup>12,13</sup> Although they are rarely mentioned in this context, previous work on MSF and DDI can be seen as approaches to multilayer networks, where the local networks are defined by the coupling between a typically small number of variables of the local dynamical system.

In the following we generalize approaches to DDI and MSF to analyze multi-layer networks of identical units with large numbers of variables. The evaluation of the local stability of stationary states leads to a block structure that permits to reduce the Jacobian to smaller matrices that can then be conveniently analyzed. The resulting equations are reminiscent of the MSF approach, albeit applied in a new context.

For illustration we consider the example of a state-of-the-art meta-foodweb model from ecology, consisting of a set of identical local foodwebs, coupled in a spatial network (Fig. 1). Here, the proposed approach reveals a MSF for the local foodweb that determines in which spatial topologies the foodweb is stable and when DDI is observed. The meta-foodweb consists of  $N$  species spreading across a network of  $M$  identical habitat patches. The population density of species  $n$  in habitat  $i$  is denoted by  $X_n^i$ , and  $\mathbf{X}^i$  is the vector of all densities in patch  $i$ . The variables change in time according to differential equations of the form

$$\dot{X}_n^i = f_n(\mathbf{X}^i) + \sum_j A_{ij} c_n(\mathbf{X}^i, \mathbf{X}^j), \quad (1)$$

where the first term,  $f_n$ , captures the effect of local interactions in the foodweb, while the second term captures the effect of migration. Here,  $c_n$  is a species-specific coupling function capturing migration, and  $\mathbf{A}$  is a weighted adjacency matrix that defines the topology of the spatial network: If two patches  $i$  and  $j$  are not connected then  $A_{ij} = 0$ , otherwise  $A_{ij} \neq 0$  is the coupling strength between patches  $i$  and  $j$ .

The approach proposed here is applicable to all systems of the form of equation (1). From an ecological perspective the stability of stationary states of the system is of particular interest. We consider the stability of a

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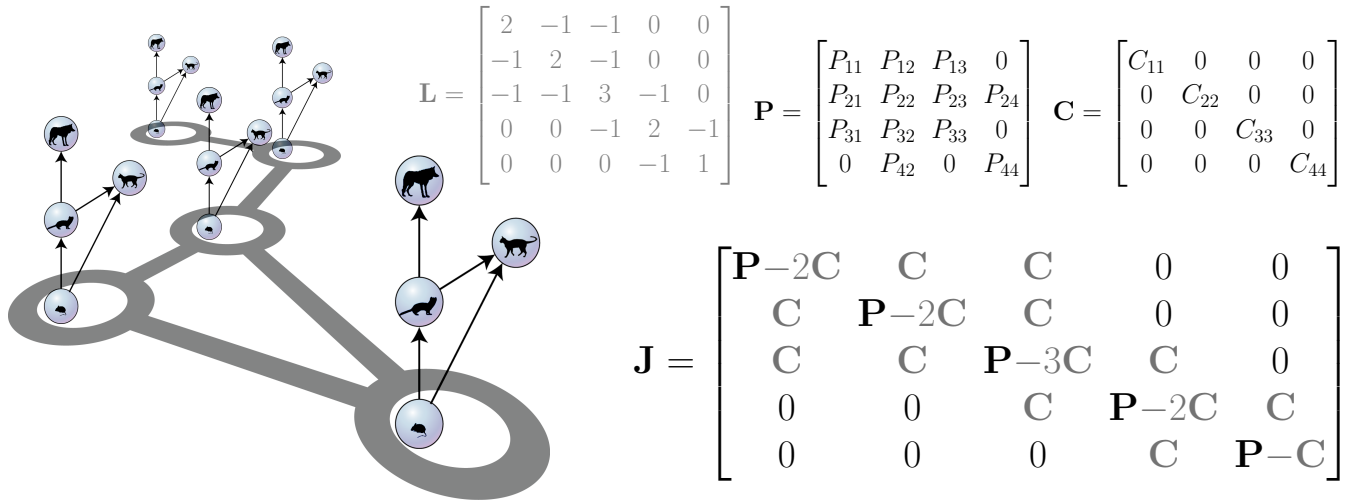


FIG. 1. Example meta-foodweb with 4 species (blue bubbles and black arrows) on 5 patches (grey lines and circles). The stability of the system is described by the  $20 \times 20$  Jacobian matrix  $\mathbf{J}$ , which can be written as  $5 \times 5$  matrix of  $4 \times 4$  blocks. The blocks contain the intra-patch Jacobian matrix  $\mathbf{P}$ , describing the dynamics within one patch, and the coupling matrix  $\mathbf{C}$ , describing the dependence of migration rates on the population sizes, which is given here for a simple diffusion process. While the intra-patch Jacobian only appears on the diagonal of  $\mathbf{J}$ , the coupling blocks  $\mathbf{C}$  occur in a pattern given by the Laplacian matrix  $\mathbf{L}$  that encodes the structure of the patch network and is shown here for a coupling strength of 1.

homogeneous state, where each species has identical densities across all patches. Such states exist under fairly general conditions, and in particular in the case where patches are coupled diffusively by link-wise dispersal.

The response of the  $NM$ -dimensional dynamical system to perturbations from the steady state can be found from a local linearization captured by the  $NM \times NM$  Jacobian matrix,

$$J_{nm}^{ij} = \left. \frac{\partial}{\partial X_m^j} \left( \frac{d}{dt} X_n^i \right) \right|_* \quad (2)$$

where the asterisk (\*) indicates evaluation in the homogeneous stationary state. Using the Generalized Modeling approach<sup>21–23</sup> the Jacobian matrix for a class of realistic food web models can be computed (see Methods). The stationary state under consideration is then stable if (and only if) all eigenvalues of the Jacobian have negative real parts.

For the type of multilayer networks considered here,  $\mathbf{J}$  has a block structure which allows us to express it as a function of a local  $N \times N$  Jacobian  $\mathbf{P}$  that captures the local dynamics within a patch, an  $N \times N$  coupling matrix  $\mathbf{C}$  that captures the effect of a given donor patch on the focal patch, and the  $M \times M$  Laplacian matrix  $L_{ij} = \delta_{ij} \sum_k A_{ik} - A_{ij}$  of the underlying network, which is a (weighted) network discretization of the Laplace operator. Using these matrices one can write the Jacobian of the system as

$$\mathbf{J} = \mathbf{I} \otimes \mathbf{P} - \mathbf{L} \otimes \mathbf{C}, \quad (3)$$

where  $\mathbf{I}$  is the  $M \times M$  identity matrix, and  $\otimes$  is the

Kronecker product.

Leveraging the block structure we can show (see Methods) that the spectrum of the Jacobian can be written as

$$\text{Ev}(\mathbf{J}) = \bigcup_{i=1}^M \text{Ev}(\mathbf{P} - \kappa_i \mathbf{C}), \quad (4)$$

where  $\text{Ev}$  denotes the eigenvalues of the respective matrix and  $\kappa_i$  is the  $i$ 's eigenvalue value of  $\mathbf{L}$ . Note that equation (4) is analogous to the corresponding equation in continuous space<sup>20</sup> where  $\kappa_i$  is replaced by the wave number, i.e. the eigenvalue of the Laplacian operator in continuous space.

Equation (4) has the useful property that the structure of the spatial networks only enters through the eigenvalues  $\kappa_i$ . This means that equation (4) defines a MSF.<sup>12,13</sup> Given only information about the local system (i.e.  $\mathbf{P}$  and  $\mathbf{C}$ ), we can compute the leading eigenvalue  $\lambda_{\max}$  that would be generated by a given Laplacian eigenvalue  $\kappa$ . The resulting function  $S(\kappa) = \text{Re}(\lambda_{\max}(\kappa))$  is then a MSF for the meta-foodweb under consideration.

Because stability requires all eigenvalues of the Jacobian to have negative real parts, stability is lost if any Laplacian eigenvalue falls into a range where the MSF is positive. In the following we refer to these ranges as “forbidden” as they have to be avoided if local stability is to be maintained.

Because different networks have different Laplacian spectra, a given food web can be stable in one geographical network and unstable in another (Fig. 2). However, once a MSF for a foodweb is known, conclusions can be

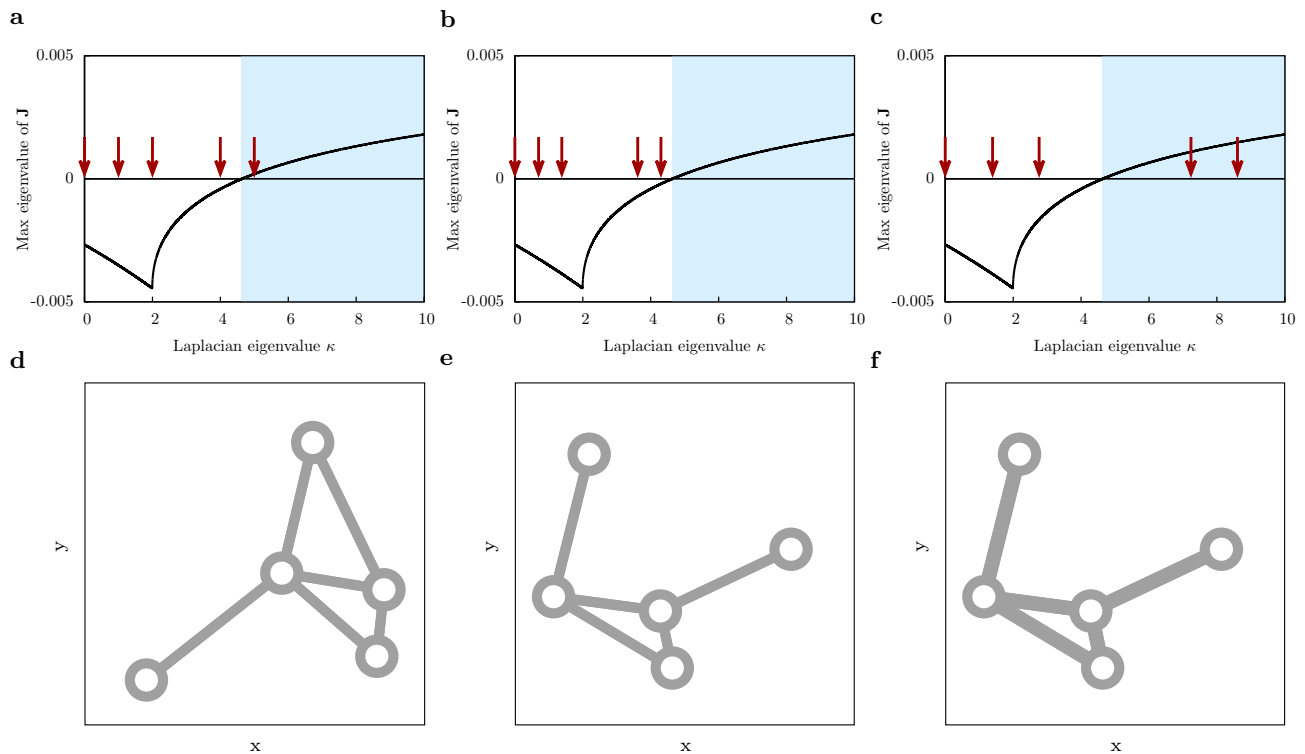


FIG. 2. Master Stability Function (MSF) for meta-foodwebs. Shown are MSFs (a-c) and spatial geometries (d-f) for the same local food web (that of Fig. 1) and coupling matrix  $\mathbf{C}$  (see Supplementary Material for details) but 3 different geometries (represented by circles, indicating patches, and lines, indicating migration links, in a two dimensional  $x, y$  landscape). The MSF (identical line in a-c) relates the Jacobian eigenvalue of the meta-foodweb to the Laplacian eigenvalue of the spacial network. The meta-foodweb is stable if none of the Laplacian eigenvalues (arrows) fall into ranges where the master stability function (line in a-c) is positive (blue shaded area). The food web under consideration is unstable on one geometry (a,d) but stable on another (b,e). Tightening the coupling (indicated by thicker lines in f) can destabilize the stable system by stretching the Laplacian spectrum (cf. b,c).

drawn by using readily available insights on Laplacian eigenvalues.<sup>24</sup> The Laplacian is a positive semidefinite matrix and hence only non-negative  $\kappa$  need to be considered. Furthermore, the Laplacian is rank deficient and thus always has at least one zero eigenvalue. Hence foodwebs for which the MSF is positive at  $\kappa = 0$  are unstable irrespective of the spatial topology. Since  $S(\kappa = 0)$  is also the leading eigenvalue of the isolated system, a meta-foodweb can only be stable if the corresponding isolated foodweb is stable.

We numerically computed the MSF for a variety of randomly generated food webs. In smaller webs with up to 5 species we mostly observed MSFs with relatively simple shapes, where the MSF is either (i) positive at zero, (ii) negative everywhere, or (iii) crosses from negative to positive values at a single  $\kappa^* > 0$  (cf. Fig. 2). The former two cases correspond to food webs that are unstable (i) or stable (ii) irrespective of the geographical network, whereas the third case (iii) is stable if all eigenvalues of the Laplacian are sufficiently small ( $\kappa_i < \kappa^*$ ). If all entries of the Laplacian matrix are multiplied by some factor, the eigenvalues scale correspondingly. Thus, in case

(iii) the homogeneous stationary state is stable if the coupling is sufficiently weak, but loses stability when the coupling strength is increased past some system-dependent threshold (cf. Fig. 2); a phenomenon that is analogous to the DDI in continuous space.

We note that the proposed approach is also applicable to non-diagonal coupling matrices  $\mathbf{C}$ . This allows us to study the case of cross-diffusion, where prey species emigrate more quickly from patches with high predator density and predators emigrate more quickly from patches with low prey density (see Supplementary Material for details). In this case complex MSF can be observed (Fig. 3). Hence, a complex sequence of stabilization and destabilization events has to be expected when the coupling strength is changed or the geographical network is modified.

In contrast to partial differential equations in continuous space, the eigenvectors of the Laplacian have a complex structure for multilayer networks. We illustrate this by considering the well-studied example of random geometric graphs,<sup>25</sup> which provide a generic model for spatial networks (see Methods). The Laplacian eigenvectors

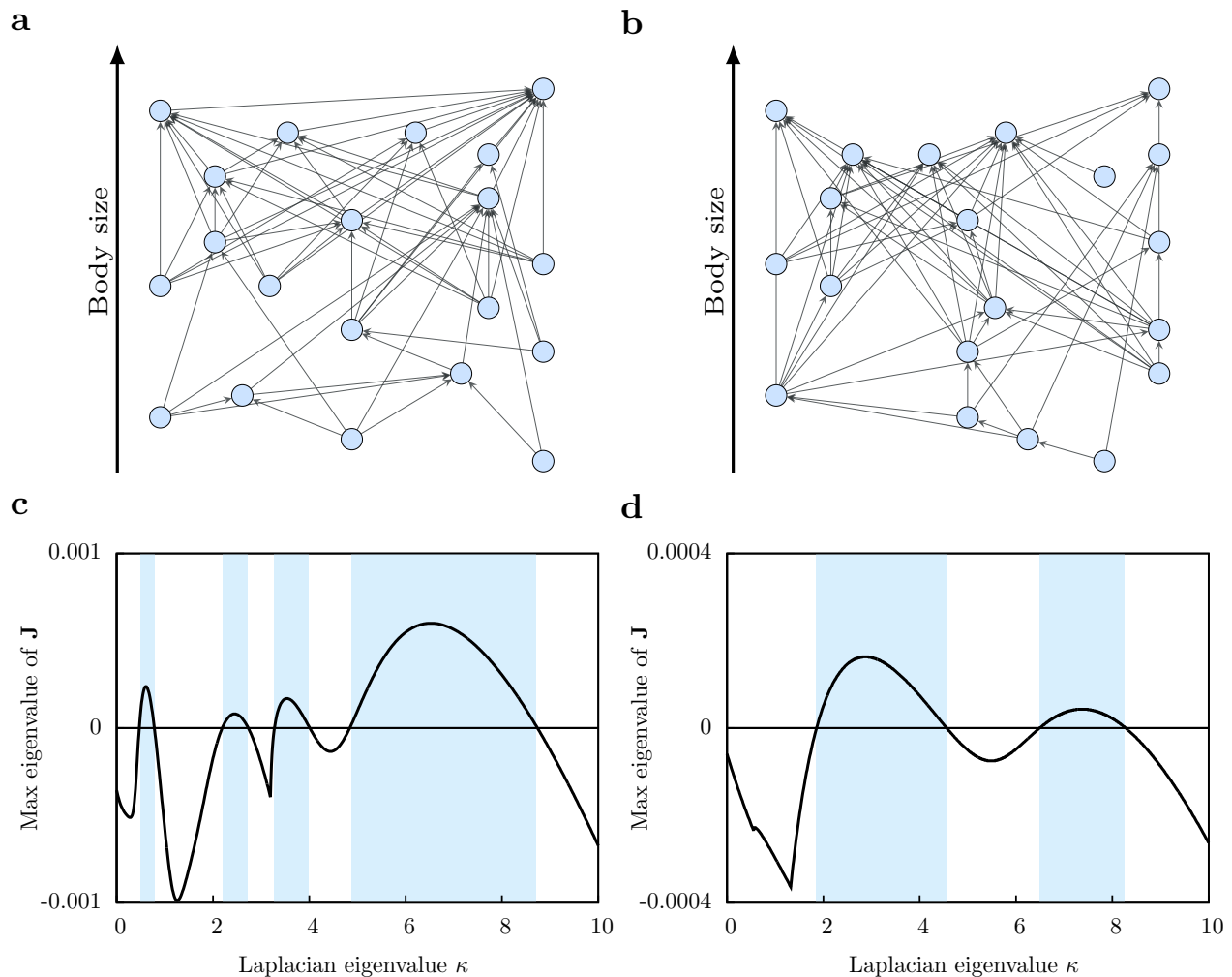


FIG. 3. Complex Master Stability Functions (MSFs). Shown are two examples of foodwebs (a,b) of 20 species (blue bubbles) connected by predator-prey interactions (arrows). The coupling matrix  $\mathbf{C}$  was constructed such that predators emigrate preferentially from patches with scarce prey and prey emigrates preferentially from patches with abundant predators (see Supplementary Material). The corresponding MSFs (c for a, d for b) have many forbidden (blue) ranges.

have the dimension of the spatial network such that each node is associated with one entry of the eigenvector. It is known that some eigenvectors are global, while the majority are localized<sup>26,27</sup> (see Fig. 4), such that they have a significant magnitude only on a small number of nodes, while being approximately or exactly<sup>28</sup> zero elsewhere. Eigenvalues only depend on the nodes in which their corresponding eigenvector has significant amplitude. We can thus say that many of the Laplacian eigenvalues *originate* from small neighborhoods in the network. Due to their specific structure (see Methods), the Jacobian eigenvectors are localized on the same nodes as the corresponding Laplacian eigenvectors. An instability triggered by the associated eigenvalue can therefore be thought of as arising from that small part of the network.

When the stationary state becomes unstable, the system will depart from it in the direction of the correspond-

ing eigenvector. In numerical explorations we found that the eigenvectors corresponding to eigenvalues in forbidden ranges are sometimes closely predictive of the final state that will be reached as the result of an instability, but this is not always the case (Fig. 4).

In summary, we studied the destabilization of the homogeneous stationary states in multilayer networks by an approach that is reminiscent of the MSF for synchronization of oscillators. The result of the loss of stability is generally a heterogeneous state. Since these states can be more diverse<sup>29</sup>, the analysis of a stable homogeneous state does not cover all situations. Thus, more research in this area is clearly necessary. The focus on the homogeneous state, inherent in MSF approaches, is the biggest limitation of the proposed approach. In the context of the ecological application “homogeneous” means identical population densities, but not patch sizes, as the effect

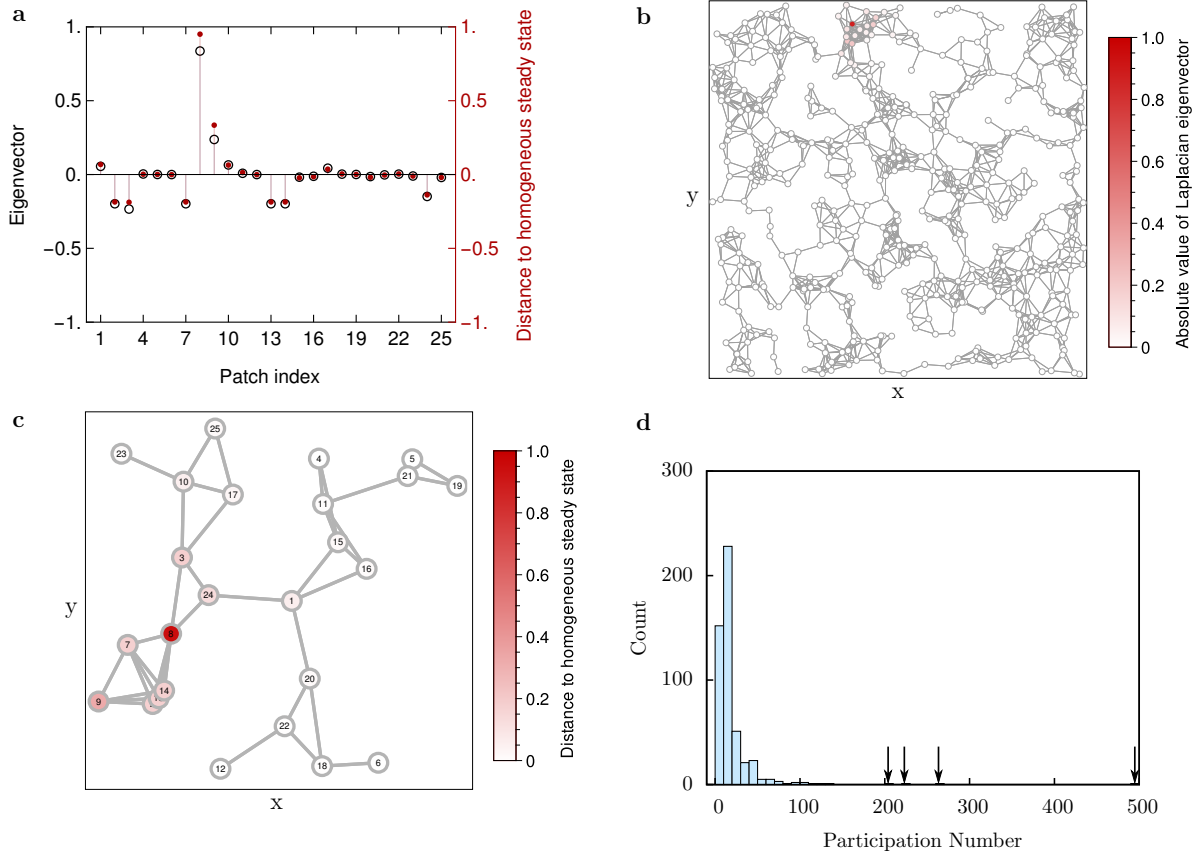


FIG. 4. Localization of Eigenvectors. Shown is a system where on a given topology (c) one eigenvalue of the Laplacian lies in one of the forbidden ranges where the MSF of the food web is positive. Hence the system departs from the homogeneous steady state and approaches a non-homogeneous state. Color-coding the distance of the density of the apex predator population to the homogeneous value (see methods) shows that the impact of the instability is confined to a relatively small area. In cases where the system approaches a state in the vicinity of the homogeneous state, the eigenvector corresponding to the destabilizing eigenvalue is indicative of the pattern in the final state. A comparison (a) of the respective eigenvector (open circles) and the observed deviation from the homogeneous value in the final state (dots) shows good agreement in the example system (c), but similar accuracy cannot be guaranteed in general. The localization of many eigenvectors is a generic feature of geographical networks. For the 500-node example geometry in b the number of nodes on which eigenvectors have a significant amplitude can be quantified by the participation number (see methods). This reveals that the majority of eigenvectors only extend to relatively few nodes (histogram in d), while only 4 eigenvalues (arrows) have significant amplitude on a large fraction of the nodes. The example shown here is a case of real eigenvalues causing a Turing instability. When the leading eigenvalue is complex, the associated instability is a wave instability (see Supplementary Material).

of size differences can be captured by the geographical network, which can be weighted and directed. Despite its limitations the approach opens up several new perspectives. For a given dynamical unit it allows to design geometries where the system is stable or unstable as desired. Conversely, in applications where there is less control over space but more control over the unit, e.g. in synthetic biology, we may be able to design the units such that undesirable spatial configurations lead to localized instabilities, which guide the system to desired configurations.

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**Data Statement.** This work did not produce or use primary research data. Details of the models can be found in the supplementary material.

**Supplementary Material.** Supplementary material is available on request from the authors.

## METHODS

### Eigenvalues of $\mathbf{J}$

Let  $\mathbf{v}$  be an eigenvector of  $\mathbf{L}$ ,

$$\mathbf{L} \cdot \mathbf{v} = \kappa \mathbf{v}, \quad (5)$$

and  $\mathbf{q}$  be an eigenvector of  $\mathbf{P} - \kappa \mathbf{C}$ ,

$$(\mathbf{P} - \kappa \mathbf{C}) \cdot \mathbf{q} = \lambda_\kappa \mathbf{q}. \quad (6)$$

In order to show that

$$\mathbf{w} \equiv \mathbf{v} \otimes \mathbf{q} = \begin{pmatrix} v_1 \mathbf{q} \\ v_2 \mathbf{q} \\ \vdots \\ v_N \mathbf{q} \end{pmatrix} \quad (7)$$

is an eigenvector of  $\mathbf{J}$  with the eigenvalue  $\lambda_\kappa$ , we exploit the fact that the Kronecker product satisfies the rule

$$(\mathbf{A} \otimes \mathbf{B}) \cdot (\mathbf{C} \otimes \mathbf{D}) = \mathbf{A} \cdot \mathbf{C} \otimes \mathbf{B} \cdot \mathbf{D}, \quad (8)$$

and obtain

$$\begin{aligned} \mathbf{J} \cdot \mathbf{w} &= (\mathbf{I} \otimes \mathbf{P} - \mathbf{L} \otimes \mathbf{C}) \cdot (\mathbf{v} \otimes \mathbf{q}) \\ &= (\mathbf{I} \otimes \mathbf{P}) \cdot (\mathbf{v} \otimes \mathbf{q}) - (\mathbf{L} \otimes \mathbf{C}) \cdot (\mathbf{v} \otimes \mathbf{q}) \\ &= \mathbf{I} \cdot \mathbf{v} \otimes \mathbf{P} \cdot \mathbf{q} - \mathbf{L} \cdot \mathbf{v} \otimes \mathbf{C} \cdot \mathbf{q} \\ &= \mathbf{v} \otimes \mathbf{P} \cdot \mathbf{q} - \kappa \mathbf{v} \otimes \mathbf{C} \cdot \mathbf{q} \\ &= \mathbf{v} \otimes (\mathbf{P} - \kappa \mathbf{C}) \cdot \mathbf{q} \\ &= \mathbf{v} \otimes \lambda_\kappa \mathbf{q} = \lambda_\kappa (\mathbf{v} \otimes \mathbf{q}) = \lambda_\kappa \mathbf{w}. \end{aligned} \quad (9)$$

### Foodweb topology

All foodwebs used in this work were generated with the niche model<sup>30</sup>, a basic topological model of food web structure. The niche model also assigns a body size to every species, which then informs biological parameters that enter in the local Jacobian and coupling matrix (see Supplementary Material for more details).

### Spatial Topologies

We considered spatial geometries that were generated as random geometric graphs<sup>25</sup>. This type of network is generated by placing the desired number of nodes on a spatial domain at locations that are chosen uniformly at random. Two nodes are linked if the Euclidian distance between them is below a specified threshold. We set the coupling strengths for all links to identical values, regardless of distance.

## Generalized food web model

Following<sup>22</sup> we assumed that the dynamics of populations is given by differential equations of the form

$$\begin{aligned} \dot{X}_i^k &= G_i^k(X_i^k) - M_i^k(X_i^k) \\ &+ \epsilon_i F_i^k(X_1^k, \dots, X_S^k) - \sum_j D_{ji}^k(X_1^k, \dots, X_S^k) \\ &+ \sum_l \left[ E_i^{kl}(X_1^k, \dots, X_S^k, X_1^l, \dots, X_S^l) \right. \\ &\quad \left. - E_i^{lk}(X_1^l, \dots, X_S^l, X_1^k, \dots, X_S^k) \right], \end{aligned} \quad (10)$$

This model encompasses generic functions for local dynamics of species  $i$  like growth by prey consumption  $F_i^k$  with an conversion efficiency of  $\epsilon$ , loss of species  $i$  by predation of species  $j$   $D_{ji}^k$ , primary production  $G_i^k$ , respiration and mortality  $M_i^k$  and inter habitat dynamics i.e. migration from habitat  $k$  to  $l$   $E_i^{lk}$ .

Without fully specifying the functions in the model, biologically sound Jacobian matrices were derived using the generalized modeling approach (see supplement).

### Explicit Model

For simulations in Fig. 4 the functions in the model were fixed to appropriate ecologically realistic nonlinear functions, such as the Holling type-II functional response for predator-prey interaction. See supplementary material for full details.

### Departure from homogeneous state

We quantify the distance of the final state of a simulation from the homogeneous steady state by focusing on one population (the apex predator) and calculating on each patch the deviation of its population density in the final state from the homogeneous steady state.

### Localization of eigenvectors

We measured the localization of a given normalized eigenvector  $\mathbf{X}$  by the participation number, defined as  $(\sum_i |X_i|^4)^{-1}$ . The participation number is a proxy for the number of nodes at which the eigenvector has a significant amplitude. In particular an eigenvector that is equally spread across  $N$  nodes, is characterized by a participation number of  $N$ .

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