

Topological conditions drive stability in meta-ecosystems

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On a global level, ecological communities are being perturbed at an unprecedented rate by human activities and environmental instabilities. Yet, we understand little about what factors facilitate or impede long-term persistence of these communities. While observational studies indicate that increased biodiversity must, somehow, be driving stability, theoretical studies have argued the exact opposite viewpoint instead. This encouraged many researchers to participate in the ongoing *diversity-stability* debate. Within this context, however, there has been a severe lack of studies that consider spatial features explicitly, even though nearly all habitats are spatially embedded. To this end, we study here the linear stability of meta-ecosystems on networks that describe how discrete patches are connected by dispersal between them. By combining results from random-matrix theory and network theory, we are able to show that there are three distinct features that underlie stability: edge density, tendency to triadic closure, and isolation or fragmentation. Our results appear to further indicate that network sparsity does not necessarily reduce stability, and that connections between patches are just as important, if not more so, to consider when studying the stability of large ecological systems.

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I. INTRODUCTION

Ecological communities with high diversity and apparent stability are crumbling under global stressors such as rising temperatures and decreasing habitat sizes [1,2]. These factors are often of human origin and have contributed to a global decline in species diversity [3,4]. Yet, while large and diverse ecosystems are ubiquitous, how these systems have assembled and why they are often so resilient is still poorly understood [5]. It is therefore vital to understand the mechanisms that enable this apparent resilience, such that these can potentially be put to use to protect endangered ecological communities.

Here, we will focus on unveiling mechanisms that might facilitate stability as resilience to perturbations. Within this context, in a seminal work May had shown that, under some assumptions, large and complex systems simply cannot be stable [6]. By assuming that species interact randomly, May could use methods from random-matrix theory to derive a *stability criterion* that determined whether a system would be stable or not. This gave rise to the well-established *diversity-stability* paradox, igniting debates across distinct scientific

communities, from theoretical physics to theoretical ecology, and for which there has not been found a definite answer [7].

However, there are some limitations in the random connectivity assumed by May: interactions among species follow more structured patterns [8–11], are subject to specific constraints [12], and in most natural habitats they are spatially extended, meaning that ecosystems are intrinsically patchy or fragmented [13,14], with local ecosystems being connected with each other through dispersal or migration [15]. When considering patches as nodes and edges as dispersal pathways between the patches [16], patchy habitats naturally form a complex network with dynamics both on and between the nodes.

The stabilizing effect of dispersal in such systems appears to rely on environmental fluctuations that are manifested in the heterogeneity of interactions such that they differ significantly between spatially distinct patches [17–19]. However, note that dispersal may even be destabilizing given the circumstances, especially in combination with trophic structure [18]. Yet, these results have been established without accounting for network structure [17,18,20]. Since ecological networks are spatially embedded [21] and may depend on species-specific dispersal kernels [22,23], the connectivity patterns might even differ depending on the species considered.

Here, we focus on the topology of patch, or dispersal, networks that comprise a *meta-ecosystem* (Fig. 1), and we show that connections between patches significantly influence the linear stability of ecological systems. In the following, we shall first introduce our meta-ecosystem model in Sec. II and

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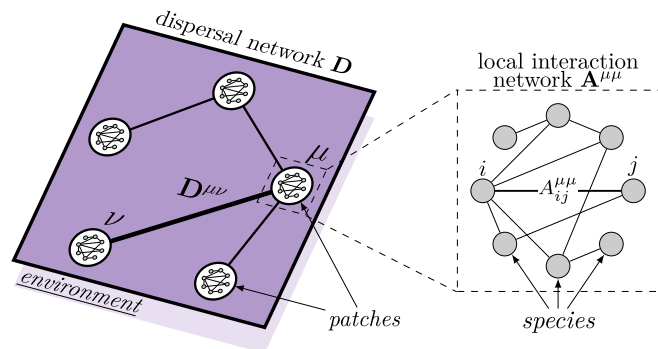


FIG. 1. Illustration of the meta-ecosystems considered in this work (see also Fig. 2). The dispersal network \mathbf{D} , and its matrix entries $\mathbf{D}^{\mu\nu}$ with elements $D_{ii}^{\mu\nu}$, capture the (rate of) exchange of species i between two connected patches, μ and ν . Within the patches, local interaction networks $\mathbf{A}^{\mu\mu}$ with elements $A_{ij}^{\mu\mu}$ capture the interaction strengths between species i and j .

establish more technical definitions of dispersal and stability in Sec. III. Thereafter, we study several distinct network topologies in Sec. IV, and we discuss our results within the context of ecosystem stability in Sec. V. Where applicable, we shall also touch upon possible ventures for experimental verification of our results.

II. META-ECOSYSTEMS AND THE COMMUNITY MATRIX

To elucidate the effects of network topology on stability, we adopt an approach similar to that of May [6] and examine the linear stability of a system resting at a hypothetical equilibrium. We note here that, although it is known that fixed point abundances influence stability (see, e.g., [24]), our aim is to compare meta-ecosystems with explicit spatial topology to those without. The effect of (steady-state) abundances is thus neglected.

We consider a meta-ecosystem with S species and M patches (Fig. 1). The ecological dispersal network captures possible dispersal pathways between the M patches. Using this network, our model assumes a community matrix \mathbf{J} of the form (see, e.g., [17,18], Fig. 2 and the Supplemental Material [25] for more details)

$$\mathbf{J} = \mathbf{R} + \mathbf{A} + \mathbf{D}, \quad (1)$$

where \mathbf{R} is a diagonal matrix representing growth, \mathbf{A} is the interaction matrix, i.e., the matrix comprised of local interaction matrices, and \mathbf{D} is a matrix that defines (species-specific) dispersal in between patches. Within this meta-ecosystem framework, \mathbf{J} has a block-structure (Fig. 2)—diagonal blocks capture within-patch dynamics while off-diagonal blocks are diagonal matrices that represent (species-specific) between-patch dispersal.

Linear, or asymptotic, stability is governed by the eigenvalues of \mathbf{J} . More specifically, the criterion for linear stability is that the largest real part of the spectrum is negative [Eq. (2)]. In the absence of dispersal (or when $M = 1$), we recover the standard and well-studied form of the community matrix [6,10,26]. For a fully connected network (all-to-all dispersal), it is possible to describe the full spectrum

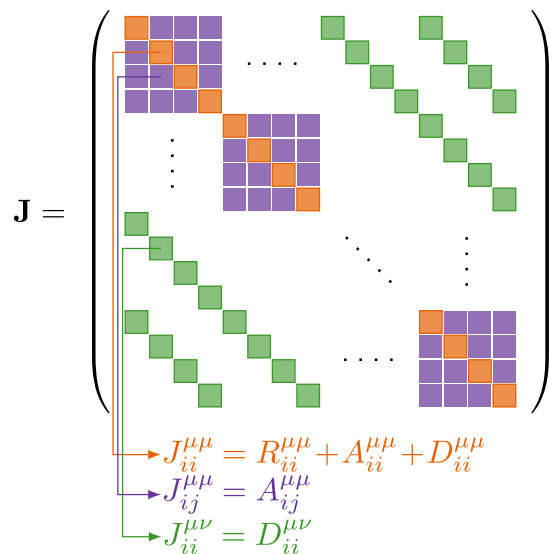


FIG. 2. Block structure of the community matrix \mathbf{J} of a meta-ecosystem with S species and M patches (see also Refs. [17,18]). Diagonal blocks of \mathbf{J} (orange, purple)—that is, $\mathbf{J}^{\mu\mu}$ —are comprised of a local (diagonal) growth matrix $\mathbf{R}^{\mu\mu}$, a local interaction matrix $\mathbf{A}^{\mu\mu}$, and a (diagonal) dispersal matrix $\mathbf{D}^{\mu\mu}$. Off-diagonal blocks (green) are themselves diagonal matrices that capture the species-specific dispersal between patches μ and ν (see also Fig. 1).

of the community matrix in a closed form, and thus to derive a stability criterion depending on dispersal [17,18]. Conversely, when dispersal occurs on heterogeneous topologies, the fully connected network model is no longer valid, and the spectra of \mathbf{J} differ significantly depending on both interactions and network topology (see Figs. 3–7), making it difficult to derive closed-form equations for the analysis. As such, we shall resort here to numerical calculations instead.

Before proceeding to study the influence of network topology on linear stability, let us specify some critical details

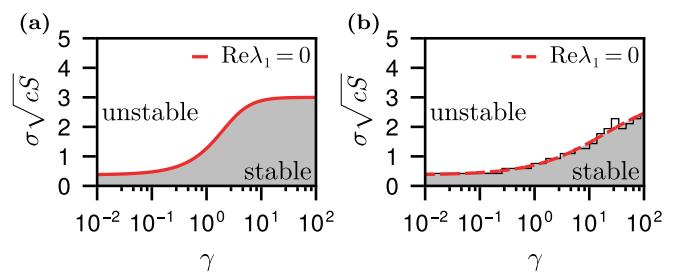


FIG. 3. Phase diagrams of stability vs the complexity, $\sigma\sqrt{cS}$ (see the text), and dispersal rate γ . Relevant parameters for both figures are $S = 128$, $M = 64$, $c = 0.2$, $r = 1$, $b = 1.375$, and $\rho = 0.0$. Note that b is chosen such that $\sigma\sqrt{cS} = 3$ for $\gamma \gg 1$. (a) Phase diagram of fully connected network. Higher dispersal rate allows for higher complexities to remain stable [see Eqs. (7) and (8)]. Red line indicates theoretical boundary at which $\text{Re}\lambda_1 = 0$ (Supplemental Material C [25]). (b) Phase diagram of cycle- or ring-network. Black lines indicate numerical approximation of the boundary at which $\text{Re}\lambda_1 = 0$, and dotted red lines are smoothed fitted curves of this boundary. Note that the complexity converges for large γ , but this is difficult to visualize due to numerical instabilities for very large γ .

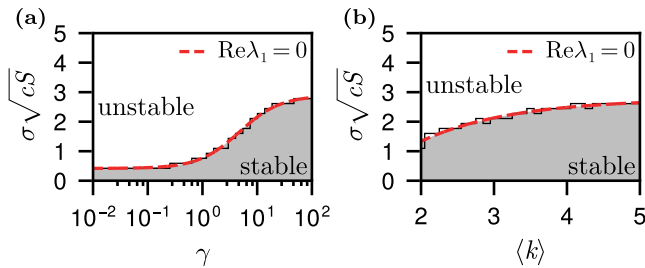


FIG. 4. Phase diagram of stability vs the complexity $\sigma\sqrt{cS}$ (see the text) and (a) the dispersal rate γ for $\langle k \rangle = 3$, and (b) the mean degree $\langle k \rangle$ for $\gamma = 10$. Patch networks are Poisson networks, meaning that they are connected and the (only) connected component has a Poisson degree distribution [Eq. (10)]. Systems are maximally spatially heterogeneous with $\rho = 0$. Black line indicates a numerical approximation of the boundary at which $\text{Re}\lambda_1 = 0$, and dotted red lines are smoothed fitted curves of this boundary. All other parameters are as in Fig. 3.

of our framework. In the following, we make a distinction between *connected networks*, networks that consist *only* of a single connected component (the giant component), and *disconnected networks*, networks that consist of more than one component. Within the context of ecological stability, this distinction is critical.

This is highlighted by, for example, considering a network that consists of a large, densely connected component that is stable, and a single isolated node. Within the context of our framework, one could conclude that the addition of a single isolated node renders the system unstable, as some of the eigenvalues corresponding to the isolated patch have a positive real part (Fig. S1) [25]. However, it is only the single isolated vertex that underlies this instability, and one should question whether a single (isolated and unstable) patch should determine the fate of the entire system.

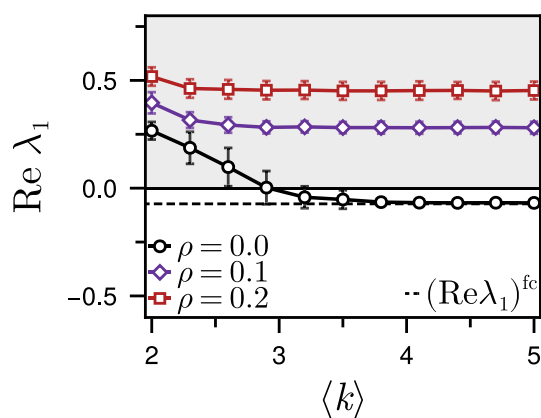


FIG. 5. Real part of the rightmost eigenvalue vs the average degree (edge density) $\langle k \rangle$ of community matrices for which the (only) giant component has a Poisson degree distribution. Different interaction heterogeneities ρ are shown. Dashed line indicates approximated value in a fully connected network (shown here for $\rho = 0$, see also Supplemental Material C [25]). Relevant parameters are $S = 100$, $M = 512$, $c = 0.2$, $r = 1$, $\sigma\sqrt{cS} = 3$, $b = r + \sigma\sqrt{cS}/M$, and $\gamma = 10$.

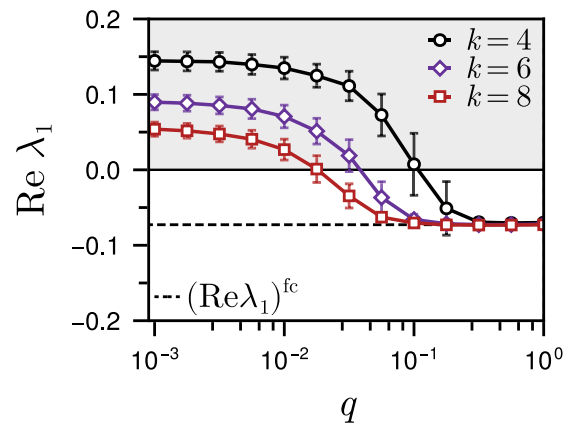


FIG. 6. Real part of the rightmost eigenvalue vs the rewiring probability q of community matrices for which the network is a Watts-Strogatz, or small-world, network. Different numbers of initial neighbors before the rewiring procedure, k , are shown (see Supplemental Material G [25]). Note that low q indicates high global clustering coefficients [Eq. (S24)]. Dashed line indicates approximated value in a fully connected network. Relevant parameters are as in Fig. 5, with $\rho = 0$.

One can then wonder if such isolated nodes should be considered part of the network or not when studying the system's linear stability. Here, we assume that permanently isolated patches should not influence macroscopical features such as equilibria and stability, and therefore we resort to studying only networks that are connected—that is, no isolated nodes exist. While this assumption is rather strict, we note that the process of becoming isolated is associated with the study of habitat fragmentation [13], which is known to decrease both population abundances and survival probabilities [1,27].

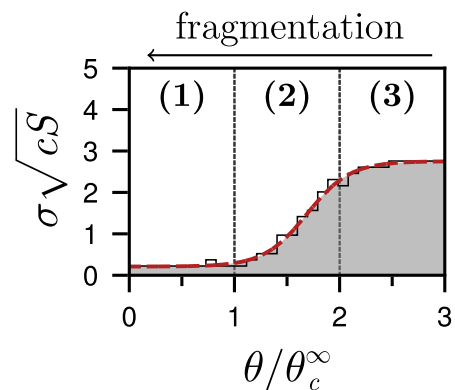


FIG. 7. Fragmentation-induced instability in random geometric graphs. Decrease in the (normalized) edge cutoff θ/θ_c^∞ can be associated with increased fragmentation. Within the phase plot we can identify three distinct regions of destabilizing mechanisms (see Fig. S10) [25]: (1) fragmentation-induced instability, originating from patches becoming isolated, (2) density-induced instability, originating from edge densities that do not allow for stable systems, and (3) complexity-induced instability, originating from too large and complex systems that cannot be stable, even with high dispersal rates and high network connectivity. Here, $S = 100$, $M = 128$, and all other parameters are as in Fig. 3.

Therefore, inclusion of isolated nodes would likely result in unstable systems regardless, and thus would not allow us to study the effects of between-patch connections on stability. A more realistic approach to relax this assumption is to take a multilayer network approach [28–30], where each layer corresponds to the dispersal network of a specific species. In this way, isolated patches in one layer might not be isolated in other layers. However, this more sophisticated framework is beyond the scope of the present work, since our main goal is to understand the role of dispersal in connected ecological patch networks.

III. DISPERSAL AND STABILITY

Let us start by considering how dispersal can potentially stabilize ecological systems. As stated earlier, linear stability is determined by (the sign of) the eigenvalues of the community matrix \mathbf{J} , which depend strongly on dispersal and ecological interaction coefficients (Fig. 2). Let us denote with $\lambda_1 \equiv \lambda_1(\mathbf{J})$ the rightmost eigenvalue of \mathbf{J} , i.e., $\lambda_1 = \max_i \operatorname{Re} \lambda_i$, where $\lambda_i \equiv \lambda_i(\mathbf{J})$ are the eigenvalues of \mathbf{J} . Then, the *stability criterion* reads

$$\operatorname{Re} \lambda_1 < 0. \quad (2)$$

Before proceeding, let us first specify the entries of the community matrix (for more details, see Supplemental Material A1 [25]). For simplicity, we consider the same growth rate r for all species, such that the growth matrix reads

$$\mathbf{R} = r\mathbf{I}. \quad (3)$$

Local interaction matrices are assumed to be random matrices, that is,

$$\mathbf{A} = -b\mathbf{I} + \mathbf{B}, \quad (4)$$

where b is the self-interaction term, and \mathbf{B} is a random block matrix with interactions between species i and j on patches μ and ν described by

$$\langle b_{ij}^\mu \rangle = 0, \quad \langle (b_{ij}^\mu)^2 \rangle = c\sigma^2/S, \quad \langle b_{ij}^\mu b_{ij}^\nu \rangle = \rho c\sigma^2/S,$$

where we have used the shorthand notation $b_{ij}^\mu \equiv b_{ij}^{\mu\mu}$, as all off-diagonal blocks are 0 (see also Fig. 2). The variance includes the *connectance* c , which is the probability that elements b_{ij}^μ are nonzero—i.e., the probability that species i and j interact on patch μ equals c . Spatial heterogeneity is manifested as a correlation between interaction coefficients between two distinct patches μ and ν of size ρ . Hence, for $\rho = 0$, interactions are i.i.d., and for $\rho = 1$ interactions are equal on each patch. We do not assume negative correlations here.

Finally, we consider homogeneous (diffusive) dispersal with a fixed rate γ . Hence, the elements of the dispersal matrix \mathbf{D} depend on the adjacency matrix \mathcal{G} of the patch network as

$$D_{ii}^{\mu\nu} = \begin{cases} -\gamma & \text{when } \mu = \nu, \\ \gamma/k_\mu & \text{when } \mathcal{G}_{\mu\nu} = 1, \end{cases} \quad (5)$$

where k_μ is the degree of patch (node) μ . Note that with this definition, we have

$$\sum_\nu D_{ii}^{\mu\nu} = 0,$$

meaning that dispersal does not bring about potential changes in species abundances. We additionally assume that dispersal is the same for all species. For further details on the elements of the community matrix, see the Supplemental Material A1 [25].

In the absence of dispersal, i.e., for $\gamma = 0$, all entries of the dispersal matrix are 0, and we recover the well-established stability criterion that May originally derived [6,9,10], which reads

$$\sigma\sqrt{cS} < b - r. \quad (6)$$

The left-hand side of this inequality is often called the *complexity* [6]. This criterion arises from random-matrix theory, according to which the eigenvalues of a random matrix with mean $r - b$ and variance $c\sigma^2/S$ all lie within a circle with center $(r - b, 0)$ and radius $\sigma\sqrt{cS}$ [10,31]. The complexity and its corresponding stability criterion imply that random systems tend to become unstable the more complex they get. Complexity can be adjusted by changing the variance of interactions, the mean number of interactions, or the number of species. As a result, it serves as a useful variable and has been studied extensively in the literature since its inception by May [6] (see, e.g., Refs. [9,26]). When dispersal is introduced, the stability criterion changes accordingly. In the case in which the patch network is fully connected, the stability criteria have been obtained previously [17,18]. For γ sufficiently small, the criterion reads

$$\sigma\sqrt{cS} < b - r + \gamma \quad (\gamma \text{ small}), \quad (7)$$

which again reduces to May's criterion for $\gamma = 0$. For γ sufficiently large, it reads instead

$$\sigma\sqrt{cS/M} < b - r \quad (\gamma \text{ large}), \quad (8)$$

which, interestingly, becomes independent of γ (but note that γ has to be large) and depends explicitly on the number of patches. It is worth mentioning that the criterion of Eq. (8) can be rewritten by isolating M . In this case, it depends on a minimum system size, i.e.,

$$M > M_{\min} = \frac{\sigma^2 c S}{(b - r)^2}. \quad (9)$$

This criterion illustrates that, when patch networks are fully connected, there need to be sufficient patches for a system to be stable. Additionally, the minimum number of patches required for stability increases with the complexity and decreases with increased self-interaction (with respect to the growth rate, i.e., $b > r$). This indicates that self-regulation is additionally stabilizing, which is in agreement with previous works [32].

A phase diagram for the full range of dispersal rates and complexities is shown in Fig. 3, for both fully connected patch networks and cycle networks. It illustrates a transition between low and high rates of dispersal, already indicating that how patches are connected affects stability.

IV. DISPERSAL NETWORKS AND STABILITY

Let us now study the eigenvalues of the community matrix when more realistic and complicated structure is considered. Recall that we consider only connected networks

whose *intraconnectivity*—i.e., *how* the nodes are connected—is defined by their degree distribution. Data on the degree distributions of ecological patch networks are, rather surprisingly, not readily available. Despite this, networks are often assumed to exhibit a wide range of degree distributions, ranging from Poisson to (truncated) power-law distributions [27,33–35], have modular [16,36] or small-world characteristics [27,35], or are explicitly spatially embedded [27,37]. However, our results shall indicate that, although the specific topology is important, the stabilizing mechanisms tend to hold across a wide variety of networks.

We initially proceed by specifying the ecological patch network as a configuration model network, i.e., a network that is generated using the configuration model (see, e.g., [38,39]), with some degree distribution $p_0(k)$ (see also Supplemental Material E [25]). As we are interested in the intraconnectivity of the giant component, we would like to control for the degree distribution corresponding to nodes in the giant component specifically, denoted with $p(k)$. To this aim, we build on recent studies on articulation points in random networks [40–42], which allow us to generate connected networks with any arbitrary degree distribution (see Supplemental Material E [25]), thus overcoming the problem related to generating networks that contain isolated patches.

A. Edge density and interaction heterogeneity increase stability

To investigate the influence of edge density and between-patch heterogeneity, let us initially consider random connected networks, named here *Poisson networks*. That is, we consider networks for which the giant component has a Poisson distribution with minimum degree $k_{\min} = 1$ (otherwise isolated patches could exist), which reads

$$p(k; s) = \frac{e^{-s} s^k}{(1 - e^{-s})k!}, \quad (10)$$

where $s = \langle k \rangle$ is the mean degree, and $1 - e^{-s}$ is the normalization constant.¹ Numerically obtained phase diagrams for spatially heterogeneous systems ($\rho = 0$) with underlying Poisson networks are shown in Fig. 4. They indicate that, as should be expected, the boundary between the stable and unstable regimes lies in between those of fully connected networks [Fig. 3(a)] and cycle networks [Fig. 3(b)]. In addition, increasing the edge density enables systems with higher complexity to remain stable.

Further inspection of the rightmost eigenvalues indicates that edge density—i.e., mean degree $\langle k \rangle$ —and between-patch heterogeneity significantly influence stability (Fig. 5). Importantly, interaction homogeneity (large ρ) can, under some circumstances, completely prevent a system from becoming stable, no matter how well connected the patches might be. This point is critical, and, while it has been established earlier in fully connected networks and cycle networks [18], our results indicate that this effect might be exaggerated in meta-ecosystems with explicit network structure.

Note that when the edge density is high, the stability criterion approaches the one mentioned earlier, as the patch network becomes closer to a fully connected network. Interestingly, the edge density that facilitates convergence to the fully connected approximation is not high, especially when compared to the density of a fully connected network $\langle k \rangle_{fc} = M - 1$. This suggests that, although edge density is important for stability, patch networks can be relatively sparse for a stable system to exist. As long as patches are sufficiently heterogeneous and density is sufficient, stable systems can emerge.

To verify this fact, we have further investigated truly sparse networks [that is, where $\langle k \rangle = O(1)$, see Supplemental Material F [25]], and we found that the above hypothesis continues to hold in these cases (Fig. S4). Therefore, patch networks that could support stable (meta-)ecosystems can be truly sparse. We note that this result is in line with the growing consensus that real-world networks are generally sparse for reasons rooted in generalized thermodynamics and information exchange [43]. While we do not study here the assembly patterns that govern ecological networks, our results do indicate that sparsity does not necessarily restrict system stability.

Within this context, we would like to touch briefly upon the impact on possible experimental verification of these results. As recent developments on microcosms allow for a detailed *in vitro* study of microbial (meta)populations (see, e.g., [44–46], among others), the apparent sparsity could justify keeping the experimental procedures simple, the reason being that one does not need to include many dispersal pathways to observe stability as if the system was to be fully connected. A possible way one could test this hypothesis is by comparing sparsely connected microcosms, e.g., using the techniques put forward in Ref. [45], to fully connected ones. The latter can be obtained by mixing all microcosms during a dilution step. We believe that such experiments can greatly enhance our understanding of stability in meta-ecosystems.

B. Clustering decreases stability

As the previously discussed topologies do not provide control over vastly different ranges of clustering (that is, global clustering coefficients or triadic closure, see Supplemental Material G [25]), we resort here to study stability in small-world networks [39,47]. These networks are constructed by starting with a regular network wherein each node has degree k , and each edge is rewired at random with probability q while avoiding self-loops and multiple edges. Note that in these networks, the edge density—that is, the total number of edges—remains fixed once the average degree is fixed, allowing us to study how the structure of the network, and in particular its clustering, influences the linear stability. However, note that allowing the density to increase does not alter the results significantly (Supplemental Material G2 [25]).

Results for the real part of the rightmost eigenvalues are shown in Fig. 6. Similar to networks with a Poissonian distribution, stability in small-world networks is improved as the density is increased for increased k . However, we can now also appreciate that a high global clustering coefficient (low q ; see, e.g., [39,47]) is detrimental towards stability. This latter result is interesting as opposite viewpoints have been reported

¹Note that the normalization constant differs from the standard Poisson distribution for which $k_{\min} = 0$.

previously [27,37]. It is important to stress, however, that the high global clustering coefficient for low q originates from the network being k -regular—that is, the dispersal network is a lattice. In metapopulation models, such regular arrangements of patches have been shown to be less stable than more random arrangements [37]. The reason for this is that more random arrangements are more likely to display spatially confined clusters that can act as sources of dispersal [37,48–50], thereby increasing the likelihood of persistence and stability.

However, note that metapopulation models [21,51], as opposed to linear models, were considered. One needs to be careful when comparing metapopulation models with the multiscale approach of a meta-ecosystems that we consider. An intuitive reason for this is that metapopulations do not take microscopic processes into account. This essentially means that some sort of mean-field approach is taken and only the total metapopulation is considered. In the underlying model presented here, instabilities can, in principle, arise from local interactions. For example, high levels of clustering do not allow weaker species—i.e., those that are generally out-competed by others—to easily migrate, hence making their extinction likely, and the full system becomes sensitive to (small) perturbation, i.e., it is unstable. When the system is instead more homogeneous, the steady state (if it exists) will most likely resemble patterns of niche-partitioning [52], and might therefore be more likely to be stable. However, as we consider here only a linearized model, we ourselves should be careful when reasoning about fixed point abundances and their effect on stability in meta-ecosystems, and we shall thus refrain from making too strong conclusions.

Finally, we would like to mention that other network characteristics, such as the mean path length, or perhaps network centralities (and their distributions) may affect system stability. We provide a more thorough investigation into the effect of the path length on stability in Supplemental Material G [25]. Using an adapted simulated annealing scheme [53] to generate dispersal networks with path lengths distinct from the small-world networks reported above, we were able to (slightly) disentangle the effects of clustering and path lengths on stability. Our results appear to indicate that clustering more significantly affects stability than path length does, and that path length only becomes a significant factor once relatively low levels of clustering have been reached. Despite this, a more in-depth study into underlying network characteristics that influence stability without an analytical motivation is difficult and is considered to be out of the scope of the present analysis.

C. Fragmentation-induced instability

The networks that we have considered up to this point are not geometric networks, meaning that patches are not spatially embedded, and there is no relevant scale associated with the length of the dispersal pathways between patches. To show that spatially explicit topologies do not drastically change our results, we consider here random geometric graphs [54]. Random geometric graphs are a specific type of spatial networks for which the vertices are distributed in space, and edges between them are established only when the (Euclidean) distance between them is lower than some cutoff θ

(Supplemental Material H [25]). When the spatial distribution of vertices is uniform, the networks are usually called random geometric networks, although more complicated or constrained distributions can be considered as well [55,56]. The number of patches M and the threshold θ define the connectivity of the network. When $\theta > \theta_c^\infty$, a giant component exists, where θ_c^∞ is the critical threshold for $M \rightarrow \infty$ [54].

Random geometric graphs are interesting as they essentially encompass three distinct topological phases: (i) a phase where most patches are isolated and no giant component exists, for $\theta < \theta_c^\infty$; (ii) a phase where a (sparsely connected) giant component emerges, yet isolated clusters of finite size remain, for $\theta > \theta_c^\infty$; and (iii) a phase where the giant component encompasses the full network and no isolated clusters exist, for $\theta \gg \theta_c^\infty$.

When studying the phase diagram of stability, we observe that these three phases correspond to three phases of induced instabilities (Fig. 7). More specifically, when $\theta < \theta_c^\infty$, patches—or clusters of patches—are isolated and are thus subjected to the destabilizing mechanisms of isolation we demonstrated earlier (Supplemental Material D [25]). Since the network is spatially embedded, patch isolation is a result of fragmentation, thus the instability that is present here is fragmentation-induced. When a giant component emerges for $\theta > \theta_c^\infty$ systems with higher complexity are able to remain stable, yet isolated clusters need to be of sufficient size [see Eq. (9) and Supplemental Material H1 [25]]. Additionally, edge densities remain low, thus this regime is associated with the density-induced instability that we additionally observed in random and small-world networks. Finally, when the giant component encompasses the full network for $\theta \gg \theta_c^\infty$, we observe behavior similar to that in Fig. 4, i.e., a higher edge density typically enables systems with higher complexity to remain stable. In this regime, the only destabilizing factor is the complexity itself.

In summary, our results are consistent with the idea that fragmentation is a destabilizing mechanism [37,57]. As increased fragmentation rates are being observed globally [58,59], these results illustrate that maintaining, or increasing, landscape connectivity is most likely key for complex ecosystems to remain stable.

V. DISCUSSION

We have presented here a study of network-related features, such as the degree distribution, connectance, and clustering coefficients, and their effects on the stability of a linear model. We considered a diverse set of different network topologies, ranging from random networks to spatial networks, where we made use of relatively recent techniques to generate connected networks with arbitrary degree distributions. In general, regardless of the degree distribution, our results indicate that increases in edge density, corresponding to a sufficient and diverse set of pathways between patches, is imperative for systems to remain stable. When focusing on networks that display high levels of clustering—i.e., the tendency to triadic closure—we found that either high global clustering coefficients or high network regularity (i.e., similarity to a lattice) contributed negatively to system stability. Finally, using spatially embedded networks, we

highlighted three distinct mechanisms that can induce instabilities; namely fragmentation-induced, edge density-induced, and complexity-induced instability. Crucially, some of these instabilities cannot be observed in fully connected systems that previous studies have considered.

While our results are promising, one major shortcoming of our model is the omission of density-dependent effects that materialize during the time evolution of the underlying dynamical model. Our assumption that the system can be linearized about a feasible steady state is quite strict and should be one of the first things to be relaxed. However, depending on the interaction structure that is considered, the stability criterion need not necessarily change [24]. In general, the stability criterion depicts an upper bound on the complexity after which a system becomes unstable. When the interaction structure is more realistic—e.g., when extracting interactions from data on food webs—there appears to still be an upper cutoff on the complexity that still allows for stability [9–11]. As the work presented here further establishes an upper bound on the complexity, now depending on the characteristics of the underlying patch network, complexity does not seem to beget stability regardless.

Within this context, while the seminal work of May [6] has spurred debate on the tradeoffs between stability and complexity, recent work has illustrated that increases in complexity might instead be actually stabilizing when sublinear growth rates are considered [60]. Including sublinear growth in the dynamical system at hand drastically changes the eigenvalue distribution, yet it is important to stress that it is likely that this effect becomes related to population density and will thus not necessarily be observed after linearization about the feasible steady state. We note, however, that in general one cannot state with certainty that density dependence changes the stability properties of the system [24]. However, when introducing nonlinear effects in the dynamics, such as extinctions, the surviving communities show distinct characteristics from the initial one [61–63], and stability measures also become more likely to be effected. While this again emphasizes the importance of including density dependence when discussing the stability and feasibility of complex ecosystems, what the effects of explicit spatial topologies will be in such systems remains an open problem.

Whereas we have considered the stabilizing effects of dispersal, dispersal can additionally be a destabilizing factor [51], as is studied in depth by Baron and Galla [18]. Within the context of meta-ecosystems, this destabilization occurs by virtue of including trophic structure, i.e., a large predator-prey system with distinct average dispersal rates for predator and prey [18]. This introduces activating components, the prey, that are inhibited by others, the predators, giving rise to Turing

instabilities—a phenomenon underlying many dynamics of pattern formation [64]. However, the potential destabilizing mechanisms of dispersal should be viewed as a separate effect from its stabilizing ones. The reason is that dispersal induced instability is associated with outliers of the eigenvalue spectrum [18]. In the systems that we have considered, which are, in essence, similar to those that Gravel *et al.* [17] considered, dispersal affects the bulk of the eigenvalue spectrum and there are no outliers. However, natural systems are clearly structured [65], and this results in outliers in the spectrum, even when omitting explicit spatial structure [11,26,66–69]. Therefore, including trophic structure in meta-ecosystems could elucidate destabilizing effects of dispersal instead, similar to those reported in Ref. [18].

Finally, our results on fragmentation-induced instability further strengthen the fact that more detailed descriptions of complex ecosystems tend to introduce more opportunities for destabilizing mechanisms [18]. Observations on the (intra)connectivity of ecological networks typically show increased fragmentation rates that effectively decrease edge density, increase patch clustering, and increase the likelihood that subsystems will become isolated [70,71]. We have shown here that all these mechanisms are destabilizing. It would be interesting to experimentally verify these destabilizing mechanisms, for example by employing recent developments in microcosm experiments [44–46]. Using these developments, one could emulate varying network characteristics by changing dispersal pathways that link distinct wells that house microbial metapopulations. The fact that our results indicate that networks need not be dense to support stable systems (Figs. 4 and 5) may simplify experimental procedures to verify this effect, yet this remains to be seen. As stability of ecological systems is for now mostly studied theoretically (but see, e.g., [72,73]), more complex studies of microcosms might reveal potential (de)stabilizing mechanisms such as those studied here.

Overall, our results indicate that if biodiversity is to be maintained, distinct patches will likely need to be ecologically rich, and diverse connections between them need to be maintained. Otherwise, these systems are unlikely to be or remain stable.

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