

## ECOLOGICAL NETWORKS

# Effects of network modularity on the spread of perturbation impact in experimental metapopulations

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Networks with a modular structure are expected to have a lower risk of global failure. However, this theoretical result has remained untested until now. We used an experimental microarthropod metapopulation to test the effect of modularity on the response to perturbation. We perturbed one local population and measured the spread of the impact of this perturbation, both within and between modules. Our results show the buffering capacity of modular networks. To assess the generality of our findings, we then analyzed a dynamical model of our system. We show that in the absence of perturbations, modularity is negatively correlated with metapopulation size. However, even when a small local perturbation occurs, this negative effect is offset by a buffering effect that protects the majority of the nodes from the perturbation.

**N**etworked systems—such as populations, ecosystems, financial markets, or air traffic—are vulnerable to perturbations that can spread, causing failure at different scales (1). The degree of vulnerability depends upon the system's network structure (2, 3). However, connectivity is a double-edged sword: Connections that in normal conditions are beneficial to the system also allow the effects of perturbation to spread (4, 5). A key question, therefore, is whether some network structures minimize the spread of perturbations.

Modularity is a network property that describes the tendency of nodes to cluster. Networks with high modularity have dense connections among nodes within modules but sparse connections to nodes in other modules. Early theory predicted that networks with a modular structure can limit the spread of perturbations, thereby promoting the stability of complex systems (6, 7). Past research quantified the degree of modularity in real networks (8–15) and simulated its effects on their dynamics (16–18). However, the idea that modularity buffers perturbations by limiting their propagation through the network has, until now, remained untested by experiment.

We conducted an experiment (Fig. 1) to assess the potential for modular network structure to constrain the spread of the impact of the perturbation across the network through time. We used 10 replicate habitat networks, each supporting large populations of the microarthropod *Folsomia candida*, a standard model organism in ecotoxicology (19). Habitat patches in the net-

work served as nodes, and movement corridors among the nodes were arranged to form the spatial modular network structure (Fig. 2A). Reproduction, mortality, and movement lead to changes in the number of individuals within the nodes of the network (20). We used automated image-recognition analysis to record and estimate the spatiotemporal dynamics of population fluctuations in the metapopulation network (21) (Fig. 2

and table S1). These laboratory networks allow for high levels of experimental control and measurement required to test the theoretical prediction that network modularity constrains the impact of perturbations.

After inoculation with 25 to 47 (median = 33) individuals (21), the local populations grew rapidly until reaching their maximum size after approximately 20 to 40 days (Fig. 2) (21). After this initial growth and establishment, a severe perturbation was imposed in half of the replicate microcosms on day 50 by removing all individuals from a single node (Fig. 2B). The perturbation resulted in immediate local population extinction. The perturbed node was maintained as a sink from day 50 until day 105 by removing all individuals that arrived into the perturbed node from adjacent nodes on a daily basis. We tracked population dynamics of each node and statistically compared the time series of the perturbed and unperturbed networks.

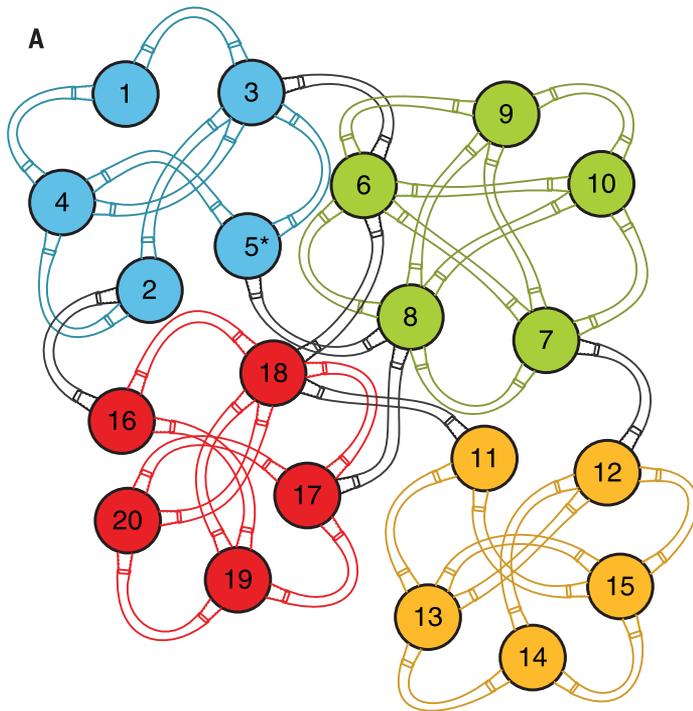
We focused on the effect of the perturbation on local population size in nearby patches to determine whether modularity constrains the spread of the perturbation across the network. To achieve this, we needed to compare the effects of the perturbation within a module versus the same effects across modules. To measure buffering, we first calculated the size of the perturbation for each node. Perturbation size is the number of individuals in the unperturbed network replicates minus the number of individuals in the perturbed replicates. We then calculated buffering



**Fig. 1. Top-down view of one of the replicate experimental networks.** The network comprises 20 vials representing nodes or habitat patches inhabited by a local population of the arthropod species *F. candida* [pictured with a stereomicroscope, size 1 to 2 mm (inset)]. These nodes are connected by tubular corridors through which the arthropods can move, creating a metapopulation occupying a network of habitat patches.

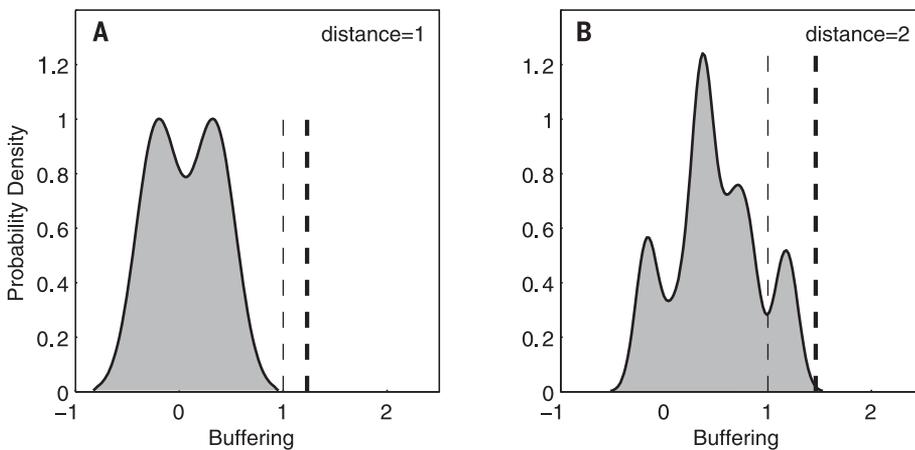
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**Fig. 2. Module partition and population dynamics in each node.** (A) Each node is identified by a number, and its color indicates the module to which it belongs. Links between modules are in black, whereas links within a module have the same color as the nodes from that module. The asterisk indicates the perturbed node. (B) Time series for each node in one of the perturbed network replicates. Lines represent the log-transformed number of individuals of each node, counted with the image processing algorithm. Line colors match the module to which those time

series belong. The shaded area shows the beginning and end of the perturbation. It is easy to see the perturbed node (5, lower blue line), where individuals were removed during the perturbation period. A low population size was maintained in node 5 because of immigration from adjacent nodes, and it recovers once the perturbation comes to an end. (C) Time series for each node in one of the unperturbed network replicates. Note that there are no extirpations in either the perturbed or unperturbed network. Final population densities differ among nodes in both (B) and (C).



**Fig. 3. Modular networks buffer the spread of perturbations.** (A and B) Probability density distribution of the average buffering values if the assignment of nodes to modules is random. The thin dashed line (buffering = 1) indicates no effect of modularity, as the decrease in the number of individuals due to the perturbation would be the same inside and outside the module to which the perturbed node belongs. The thick dashed line indicates the average observed buffering of the module assignment maximizing modularity. Panels (A) and (B) correspond to distances from the perturbed node of one and two links, respectively. We include randomizations only where the number of nodes inside and outside is the same as in the assignment within the experimental microcosms.

as the ratio between perturbation sizes inside and outside the module to which the perturbed node belongs.

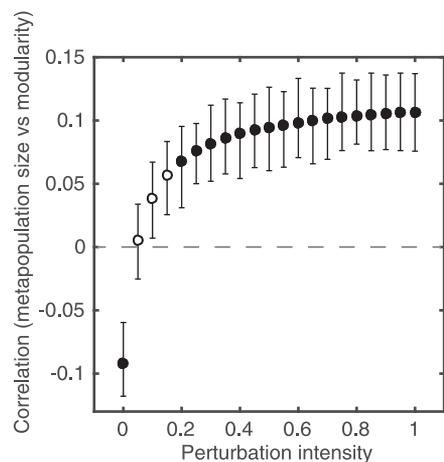
This measure of the buffering effect indicates how many times there are more individuals out-

side the module where the perturbation begins versus inside that module (21). We observed that, as predicted by theory, modules confine the spread of the perturbation (Fig. 3). Population sizes were reduced to a lesser extent in nodes

located outside the module to which the perturbed node belongs. On average, this reduction amounts to 23% ( $t = 0.87$ ,  $P = 0.38$ ) when the local population is separated from the perturbed node by a distance of one link and to 46% ( $t = 3.04$ ,  $P = 0.002$ ; one-tailed, paired  $t$  test) when separated by a distance of two links (21) (fig. S20).

At this point, however, we could not be certain about whether modularity is the network property responsible for this result because our experiment included only one network configuration. One way to verify that modularity is the driving factor is to compare the observed results with those obtained with different assignments of nodes to modules. We originally assigned nodes to modules in a way that maximized modularity. We next examined whether any other assignment of nodes to modules could have returned a similar or even greater degree of buffering. To do this, we calculated the buffering effects after randomizing the node-module assignment (21). Our results (Fig. 3) show that assigning nodes to modules in a way that maximizes modularity results in the largest buffering effect. We conclude, therefore, that network modularity buffered the spread of perturbations in these experiments.

Our experimental result is constrained by network size and configuration, so we next explored the generality of our results by using a metapopulation model of *F. candida* in habitat networks.



**Fig. 4. Perturbation intensity mediates the overall effect of modularity.** The simulations show that modularity has a positive effect on total metapopulation size only in the presence of perturbations. Perturbation intensity is measured as the fraction of individuals removed from node 5—we perturbed this node to recreate *in silico* the experimental setting. The relationship between network modularity and the total number of individuals inhabiting the metapopulation is measured as Spearman correlation coefficients. Solid symbols are statistically significant Spearman correlation coefficients ( $P < 0.05$ ), whereas open symbols are not statistically significant ( $P > 0.05$ ). The dashed line is a visual aid to differentiate between negative and positive correlation coefficients. To estimate the standard deviation (error bars) for the correlation values, we subsampled pairs of values of correlation magnitude and perturbation intensity. We created 100 subsamples without replacement of half the length of the original set of values.

Using exactly the same network configuration as in the experiments, we show that we obtain the same results when we change the node where the perturbation occurs (21) (fig. S19).

We then examined the effects of the perturbation at greater distances from the targeted patch. For that, we used simulated networks with the same degree distribution as the experimental networks but with a thousand nodes and with variable modularity and perturbation intensities (21) (fig. S21). With this approach, we first go back to the observed result of buffering being greater at a distance of two links, as opposed to one link, from the perturbation. Our simulations indicate a nonlinear increasing relationship between network modularity and the average buffering effect (fig. S22), and this effect increases markedly with distance from the perturbed node. This result confirms our experimental finding and extends it across a range of network sizes. Modularity is therefore a major determinant of the spread of a perturbation in these metapopulation networks.

Next, we used our simulations to assess the extent to which the observed beneficial role of modularity in containing perturbations is medi-

ated by the intensity of perturbations. Although we did not observe population extinctions, small population sizes are correlated with high extinction risk (22). Populations within a module where a perturbation originates are expected to have a greater risk of extinction. Modularity constrains dispersal within the module, hindering network-wide dispersal. This may reduce total metapopulation size in comparison with a configuration in which dispersal occurs at the scale of the entire network, allowing individuals to easily disperse to any other node (23). It is unclear, therefore, whether a trade-off exists between modularity-driven population persistence and overall network population size, as well as whether perturbations favor modular networks. To explore this trade-off, we simulated metapopulations with the same number of nodes and subject to the same perturbation as those of the experiments but with different modularity values—achieved by increasingly randomizing the original network while keeping constant the degree of each node (24). The results of these simulations corroborate our experimental result. We find that increasing modularity leads to a stronger buffering effect against perturbations (21) (fig. S23). We find a positive correlation between overall network metapopulation size and the degree of modularity, and this correlation strengthens with increasing link distance from the perturbation. The positive correlation between modularity and metapopulation size occurs only in the presence of perturbations, and this correlation increases asymptotically as perturbation intensity increases (Fig. 4). However, in unperturbed networks, total network population size decreases as modularity increases. Therefore, modularity comes at a cost to network metapopulation size in unperturbed systems. However, when a perturbation occurs, even when it is small and localized to a single node, modularity permits a larger overall metapopulation size. Therefore, the dynamical implications of modularity have to be assessed in light of the likelihood and intensity of the perturbations the system has to face.

Human-dominated landscapes are increasingly fragmented into habitat networks of varying spatial complexity and connectivity (25). Population extinction can occur as habitat is lost and perturbations spread through networks of habitat fragments. We have shown that spatial modularity is a crucial aspect of habitat network connectivity that affects the likelihood of population persistence despite unpredictable perturbations. Our findings suggest that network-based approaches to conservation should be considered when restoring connectivity in heavily fragmented landscapes (26, 27), when designing protected areas (28), or when limiting the expansion of a disease outbreak (29). In all of these scenarios, spatial modularity can be managed in habitat networks to reduce the cascading impacts of perturbations that may drive extinction and threaten biodiversity. Our demonstration of the buffering effect offered by a modular structure during perturbation also has implications for other fields in which networks are good descriptors of

the system's structure. One such field is finance, where the recent global crisis has led to the suggestion that managing network modularity may reduce systemic risk (1, 30, 31). The interplay between experimental and simulated networks used here confirmed the value of understanding how network structure limits the impact of a perturbation.

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## SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/357/6347/199/suppl/DC1  
Materials and Methods  
Supplementary Text  
Figs. S1 to S25  
Table S1  
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### Modularity limits disturbance effects

The networks that form natural, social, and technological systems are vulnerable to the spreading impacts of perturbations. Theory predicts that networks with a clustered or modular structure—where nodes within a module interact more frequently than they do with nodes in other modules—might contain a perturbation, preventing it from spreading to the entire network. Gilarranz *et al.* conducted experiments with networked populations of springtail (*Folsomia candida*) microarthropods to show that modularity limits the impact of a local extinction on neighboring nodes (see the Perspective by Sales-Pardo). In networks with high modularity, the perturbation was contained within the targeted module, and its impact did not spread to nodes beyond it. However, simulations revealed that modularity is beneficial to the network only when perturbations are present; otherwise, it hinders population growth.

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